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Wildlife trade at the interface between deeply-rooted animal-based traditional medicine and unregulated harvesting of wild animals in West Africa

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Local trade remains a data poor component of wildlife crime that must be better understood for more effective combat against the illegal wildlife trade. We assessed the distribution of wildlife markets, diversity of species traded and the extent of the trade chain through spatial analysis of wildlife sale sites and semi-structured interviews with 75 vendors in the 10 largest traditional medicine markets of Benin. GPS coordinates of wildlife markets were used to map their geographic distribution and assess their spatial patterns. We used a generalized linear model to determine the drivers underlying the spatial patterns of wildlife markets. A circular layout was designed to delineate the geographic extent of wildlife trade in terms of supplying sources. We found that wildlife was traded at 121 sale sites in Benin, highly dominated by traditional medicine markets (106 sites). The spatial analysis of markets exhibited an aggregative distribution pattern, and the type of market, the number of stalls in the markets and the municipality status influence significantly the spatial temporality of market distribution. Wildlife trade for traditional medicine affected 268, 96 and 61 bird, mammal and reptile species, respectively, and included species of both high national and global conservation concern. We also found that the national wildlife trade in Benin was supplied from 80% (12/15) West African Economic and Monetary countries, and all the Economic Community of West African States (except Guinea-Bissau) in violation of national laws, CITES, and regional commitments to combat wildlife trafficking (e.g., the West African Strategy for Combatting Wildlife Crime). Our study in Benin is a big step to revealing trade throughout in West Africa. It provides much needed information on wildlife trade structure and driving forces that could help to inform decision-making for better trade regulation and for effective wildlife law enforcement in West Africa. Other studies should do the same to help paint a more complete picture of wildlife trade in West Africa.

KEYWORDS

birds, law enforcement, mammals, reptiles, spatial distribution, wildlife crime, wildlife markets

Introduction

Biodiversity is a traditionally valued resource used to meet fundamental needs, particularly in the tropics where conservation and poverty alleviation represent two major challenges (Robinson and Bennett, 2002; Lee et al., 2020; Ingram et al., 2021). Throughout the tropics, people depend on wildlife to varying degrees for their food, traditional medicine, cultural practices and income (Robinson and Bennett, 2002; Brashares et al., 2011; Lee et al., 2020; Ingram et al., 2021; Booth et al., 2021). However, the use and trade are not governed effectively by either formal or informal means. Human populations and their needs have been steadily growing, leading to overexploitation being a major driver of decline and consequently biodiversity loss (Alves and Rosa, 2007; Joppa et al., 2016; Maxwell et al., 2016; Benítez-López et al., 2017; Ripple et al., 2017).

Wildlife trade, comprising local, domestic and international, generally includes species of both protected and unprotected status under national and international legislation (Nikolaus, 2011; Djagoun et al., 2013; Buij et al., 2016; Petrozzi, 2018; D'Cruze et al., 2020; Zanvo et al., 2021a, 2022). International trade has been shown to affect > 6,000 species, including a diversity of birds (8.5%), mammals (23%) and reptiles (21.3%) and, over the last two decades (UNODC, 2020). Domestically, especially in sub-Saharan Africa, wildlife trade is deep-rooted and manifests through bushmeat markets (BM) and traditional medicine markets (TMM). Trade in BM is largely in native (either nationally or regionally), wild species and largely for consumption (Lee et al., 2020; Booth et al., 2021; Ingram et al., 2021), while TMM trade a more diverse set of body parts of both wild and domestic species, including native and non-native, for medicinal and spiritual (religious and occult) purposes (Nikolaus, 2011; Djagoun et al., 2013; Lee et al., 2020). Though these markets play important roles in local community livelihoods, traditional medicine and the maintenance of endogenous religions (*Vodùn*) throughout West Africa (Alexander et al., 2015), they also represent a major driver of defaunation and biodiversity erosion in the region (Djagoun et al., 2013; Petrozzi et al., 2016; Petrozzi, 2018; D'Cruze et al., 2020). Previous authors have estimated that the bushmeat trade affects *c.* 500 species with extraction volumes that reached c. 4.9M tons per year in Africa and suggested it is very likely unsustainable (Fa et al., 2002; Redmond, 2006). Similarly, TMM affect as many as 100 mammal (Djagoun et al., 2013; Petrozzi et al., 2016) and 302 bird species (Petrozzi, 2018) across West Africa. Recent studies in West Africa revealed that TMM affects 15 bird species, 16 mammal species and 8 reptile species in Ghana (Gbogbo and Daniels, 2019) and 2 bird species, 22 mammal species and 2 reptile species in Togo (Sonhaye-Ouyé et al., 2022). This taxonomic diversity of wild species traded in TMM included endangered species such as vultures, pangolins, elephants etc. that their loss could have devasting impacts on African's ecosystems (Chao et al., 2020; Carucci et al., 2022; van de Water et al., 2022) and a consequently on climate change (see Bello et al., 2015). Though mostly domestic in nature, transboundary regional trade represents a violation of the CITES treaty, and 79% (11,645/14,741) of species having a biological resource use recorded in the CITES trade database are listed on the IUCN Red List with local trade as a threat (Challender et al., 2023). In spite of this, local trade of wildlife via BM and TMM remains the poorly studied components of wildlife crime, particularly in West Africa (UNODC, 2020) and specially when compared to Central Africa (Taylor et al., 2015).

In West Africa, the little data available on wildlife trade at the local/national scale is mainly focused on internationally protected species (Zanvo et al., 2021a, 2022), single taxonomic groups (e.g., birds, mammals or reptiles), and mostly with restricted spatial scope (e.g., to a single market or city) (Nikolaus, 2011; Djagoun et al., 2013; Williams et al., 2014; Buij et al., 2016; Petrozzi, 2018). To our knowledge, no field-based study has thus far addressed local/or domestic wildlife trade at a national scale for any country in the region but also in Africa. This lack of data renders understanding of the interplay between national and international trade impossible, in spite of recommendations to do so (Ingram et al., 2021). Such an increased understanding will improve law enforcement efforts by significantly reducing the risk of targeting wrong places and wrong species (see UNODC, 2020).

Even though Benin has been identified as one of the West African countries most involved in the regional wildlife trade (Williams et al., 2014; Buij et al., 2016) including some high concern species, the local trade had never been deciphered at a country-wide scale using the three animal taxonomic groups (birds, mammals and reptiles) most threatened by international trade (UNODC, 2020) simultaneously. The number of wildlife markets, their spatial distribution and the drivers underlying their spatial pattern are still largely unknown. The sources of bird, mammal and reptile specimens sold openly in these markets remains understudied. Such data are prerequisites for effective regulation of hunting activities, regional coordination of efforts to tackle wildlife crime, effective law enforcement at the national scale, and enlightened combat against transnational organised crime. They could help to better understand the geographic and functional connectivity of local/national trade and regional wildlife trade, and are essential for international cooperation.

This study constitutes the first country-wide field-based investigations of local trade in wildlife using the three most targeted animal groups by international trade. We provide details on wildlife trade at a national scale through the distribution of wildlife markets, the diversity of species traded and the extent of the trafficking chain in Benin. Here we aimed to: (i) investigate the spatial distribution pattern of wildlife markets and factors underpinning the pattern, (ii) assess the diversity and conservation profiles of mammals, reptiles and birds openly traded in the wildlife markets, and (iii) assess the sources of these taxa traded in the wildlife markets.

Methods

Study area

We conducted the study from July 2019 to December 2021 in the Republic of Benin, a West African country that covers the largest landscape in the Dahomey Gap. It is located between latitudes 6°25'-12°25' N and longitudes 0°45'-3°55' E, including 77 districts and

shares its terrestrial borders with Nigeria, Togo, Niger and Burkina Faso to the east, west, north and northwest, respectively. Benin is subdivided into three ecological regions (White, 1983): the Guineo-Congolian zone between 6°25-7°15' N and under bimodal rainfalls, the Soudano-Guinean zone extending 7°15'-9°45' N and the Sudanian zone between 9°45'-12°25', both characterized by unimodal rainfalls. An estimated human population of *c.* 12 M inhabitants (INSAE, 2013) is distributed across a landscape of 114,673 km^2 with the highest population density in southern Benin. The country counts 56 protected areas unequally distributed following the latitudinal gradient and representing 26% of total land area. Benin scores second highest on the global religious diversity index (Lin et al., 2022), including the native, widespread, and dominant religion '*Vodùn*'. This traditional religion is animal-consuming and commonly practiced by all the ethnic groups in Benin. It has persisted despite the rapid uptake and growth of foreign expansionist religions (Christianity and Islam) driven by colonization and globalization (Lin et al., 2022). Apart from the endogenous '*Vodùn*' religion, Christianity and Islam are the most widely practiced religions in the south-central and northern regions respectively. Of the 42 ethnic groups in Benin, the Fon, Adja, Gun, Nago and Yoruba are the largest in southern and central Benin, while the Bariba, Dendi, Otamari and Yoa Lokpa are the dominant ethnic groups in northern Benin (INSAE, 2013). The precarious healthcare system (850 private and public hospitals, 1.2 doctors per 10,000 inhabitants) is officially oriented towards western medicine (Sylvest, 2013) less accessible to impoverished population alongside an affordable traditional medicine.

Data collection

To conduct our investigations in the TMM, we obtained the written consent from authorities of the animal-based traditional medicine Association [*Association des Guérisseurs et Prêtes Endogènes de la Collectivité Awinon* (AGPECA)] including vendors in both Benin and Togo, and verbal consents of all the participants included in this study. Although the vendors have never been harassed (repression) by the wildlife trade enforcement services due to the cultural aspect of traditional medicine markets, all participants were guaranteed confidentiality and anonymity due to sensitive information collected in the framework of the study. This was necessary to motivate participants to provide reliable information.

We started our data collection by georeferencing of all the wildlife markets across Benin using the snowball technique (Berg, 2001) and districts as sampling units. Within Benin's 77 districts, we georeferenced all the wildlife markets, categorized each by type (BM/TMM), temporality (permanent/periodic), and quantified the number of all stalls. The permanent markets operate every day while the periodic markets operate every 4 or 5 days. BM are dedicated to the fresh or smoked wild meat trade for consumption whereas TMM are dedicated to the trade of dry specimens including both whole individuals and animal body parts processed by traditional and/or modern techniques for long-term preservation (Zanvo et al., 2021b). The latter makes identification of specimens in TMM in particularly challenging.

Prior to entering markets, we generated a list of potential species (birds, mammals and reptiles) we might observe within each of the three target taxonomic groups, including both local and scientific names. We generated these lists using the Red List for Benin (Neuenschwander et al., 2011), the Biodiversity Atlas of Benin (Sinsin and Kampmann, 2010), and other published taxonomic references for the region (e.g., Ullenbruch et al., 2010; Djagoun et al., 2013; Petrozzi, 2018). Local names were listed in the *Fon* language because most of our targeted markets were located in southern and central Benin and that almost all the stakeholders in these TMM belong to *Fon* ethnic group (Zanvo et al., 2021a). We recorded additional local names through pilot investigations using posters and focus groups in three larger markets from Atlantic and Littoral districts.

We then carried out individual semi-structured interviews with 75 vendors in 10 TMM, including markets in the southern (6), central (3) and northern (1) regions. These markets were those comprising a great number of stalls (≥15 stalls), except in the northern part where we were not able to conduct the wildlife species inventory and any other activities in the largest market of Manlanville, because vendors did not give us their agreement through verbal consents. The interviewees were all adult men, randomly selected without controlling for stall size and education level. We conducted each interview after we had explained the objectives of the study and then obtaining verbal consent to participate. We asked each interviewee to confirm the presence or absence of each species on our list in his stall at the time of the interview. For any species not present at the time of the interview, we asked the vendor to confirm if they had previously sold at least one specimen of that species during the last two years. We further allowed each interviewee to add species not on our list that were present at the time of interview and/or had been traded during the last two years. We limited the time period to up two years to avoid the bias related to the Local Ecological Knowledge (LEK) degradation over time (Aswani et al., 2018). We finally asked the vendors to indicate the country of origin of specimens observed in the stalls at the time of the interview. The three lists of potential species for the three taxonomic groups were administrated at different time periods and according to the interviewees' availability in order to allow each respondent to remain lucid during the surveys. In addition, we swapped the order of implementation of our three lists from one interviewee to another one. This strategy was used to get the same data quality for the different taxonomic groups.

Data analysis

In order to assess the spatial pattern of wildlife sales, we mapped the different types of markets using ArcGis 10.8.1 (Esri France) and analyzed the randomness of their distribution under point process theory (Ripley, 1981) using the PCF function of the *spatstat* package in R.4.2.1. This function provides the probability density of the g function under the Complete Spatial Randomness null hypothesis. We delineated the spatial distribution pattern through the univariate g(r) function, where *r* is the spatial scale and the g(r) function, the

ratio of the expected number of markets to the density of sample markets in a circle with any markets across Benin. We computed the function $g_{obs}(r)$ using 10,000 simulations at the 5% confidence interval and compared it to the theoretical function $g_{theo}(r)$ under the null hypothesis [g(r) = 1]. Rejection limits for the test are estimated as the envelopes of simulations and in the event that g(r) was, for a given scale r, outside the simulation envelopes, the null hypothesis was rejected at this scale. So, g(r) = 1 indicates randomness, while g(r) > 1 and g(r) < 1 indicate clumping and regularity, respectively. We calculated the mean number of stalls for BM and TMM, and estimated the density of markets for each ecological zone (Guineo-Congolian, Soudano-Guinean and Soudanian).

To identify the relevant factors underlying the spatial distribution pattern of wildlife markets, we used a generalized linear model with binomial error and logit link to explain the temporality of wildlife markets (permanent *vs.* periodic) in response to the status of the municipality in which each market occurs (special, intermediate and ordinary), the ecological zone in which each market occurs (Guineo-Congolian, Soudano-Guinean and Soudanian), the number of stalls recorded market, the type of wildlife market (BM/TMM), and the Euclidian distance from wildlife markets to the nearest protected area under the management of government officials. We used the Pearson correlation coefficient to first assess collinearity among the predictor variables. The status of the municipality in which each market occurs was determined following the ordinance categorizing the municipalities in Benin (*DÉCRET N° 2022-319 DU 1er JUlN 2022 fixant les critères de catégorisation des communes and DÉCRET N° 2022- 320 DU 1er JUIN 2022 portant catégorisation*). According to the ordinance "*DÉCRET N° 2022-319 DU 1er JUlN 2022 fixant les critères de catégorisation des communes*", the status of municipalities was defined as followed: (i) "special status," scored (3), is a municipality with at least 200,000 inhabitants and that has mobilized over a period of at least three years preceding the year of evaluation of the municipalities' categorization of budgetary resource amounting to one billion FCFA (1 Euro = 655 FCFA; the local currency) at least every year, (ii) "intermediate status," scored (2), is a capital of a district that played a leading role in the history of Benin, having a population of at least 100 000 inhabitants and mobilized in a period of at least three years preceding the year of evaluation its own budgetary resource amounting to five hundred million FCFA at least each year, and (iii) "ordinary status," scored (1), includes all other municipalities that do not belong to categories (i) and (ii).

To understand the amplitude of threats related to the wildlife trade, we visualized the percentage of recorded bird, mammal and reptile species in the 10 TMM in each of the following "protected" classifications. To understand the prevalence of threatened taxa, we annotated each recorded species with its IUCN Red List of Threatened Species (IUCN, 2022; https://www.iucnredlist.org) status, as well as its national Red List status for Benin (Neuenschwander et al., 2011). We also used the IUCN Red List to annotate each species as native or non-native to Benin. To understand the prevalence of protected species, we annotated each recorded species by its national status under Law N° 2002-16 of 18 October 2004 on wildlife protection in Benin and ordinance N° 2011-394 of 28 May 2011, which define the modalities for species and habitat conservation and sustainable management in Benin. Each species was recorded as either Integrally Protected (category A), which cannot be hunted; Partially Protected (category B), which may be hunted outside protected areas; or not listed (category C), which generally are not protected or managed under Benin law. Finally, to understand the prevalence of species who's transboundary trade should be managed under the terms of the Convention on International Trade in Endangered Species (CITES), we also annotated each recorded species by its CITES appendix (UNEP-WCMC (Comps.), 2022; http://checklist.cites). For each of these "protected" classifications, we visualized the proportions using histograms in Excel.

To decipher the trade network related to local trade, the source countries (origins of specimens as indicated by traders) collected from 590, 609, and 609 birds, mammals and reptiles specimens respectively in the stalls at the time of interviews were used to delineate the geographic extent of the trade and the contribution of each country to the local trade using a circular layout designed from ChordDiagram function in the package *circlize* (Gu, 2021). We used Pearson's Chi-squared test to compare the frequency of citation between taxonomic groups.

Results

Wildlife market spatial temporality

We recorded 121 wildlife markets in Benin, including 106 TMM and 15 BM (Figure 1). The mean number of stalls in the TMM and BM were 5.83 and 1.2, respectively. Among TMM, the biggest wildlife markets were Dantokpa (56 stalls, Southern Benin), Avogbannan (36 stalls, Southern Benin), Gbèdagba (34 stalls, Southern Benin), Malanville (30 stalls, Northern Benin) and Azovè (26, Southern Benin). We observed a latitudinal trend in the density of wildlife markets, with the higher wildlife market density (1 wildlife market/267km^2) in the Guineo-Congolian zone in the south and lower wildlife market density in the Soudanian zone (1 wildlife market/1877km^2) of the north. The univariate spatial distribution of all wildlife markets (BM and TMM) exhibited aggregative distribution patterns across Benin (Figure 2).

We found that the municipality status (e.g., special, intermediary and ordinary), number of stalls and the type of market (BM and TMM) were all significant predictors of wildlife market temporality (permanent *vs.* periodic) in Benin (Table 1). In other words, permanent markets mostly occurred in biggest municipalities (special status) and had the highest numbers of stalls. There was also a higher probability that BM were permanent compared to TMM.

Diversity and conservation status of traded species

We observed and/or detected through interviews 268, 96 and 59 species of birds, mammals and reptiles, respectively (Supplementary Tables S1–S3, Supplementary Material). The species diversity recorded in TMM comprised 27, 5 and 8 non-native bird, mammal and reptile

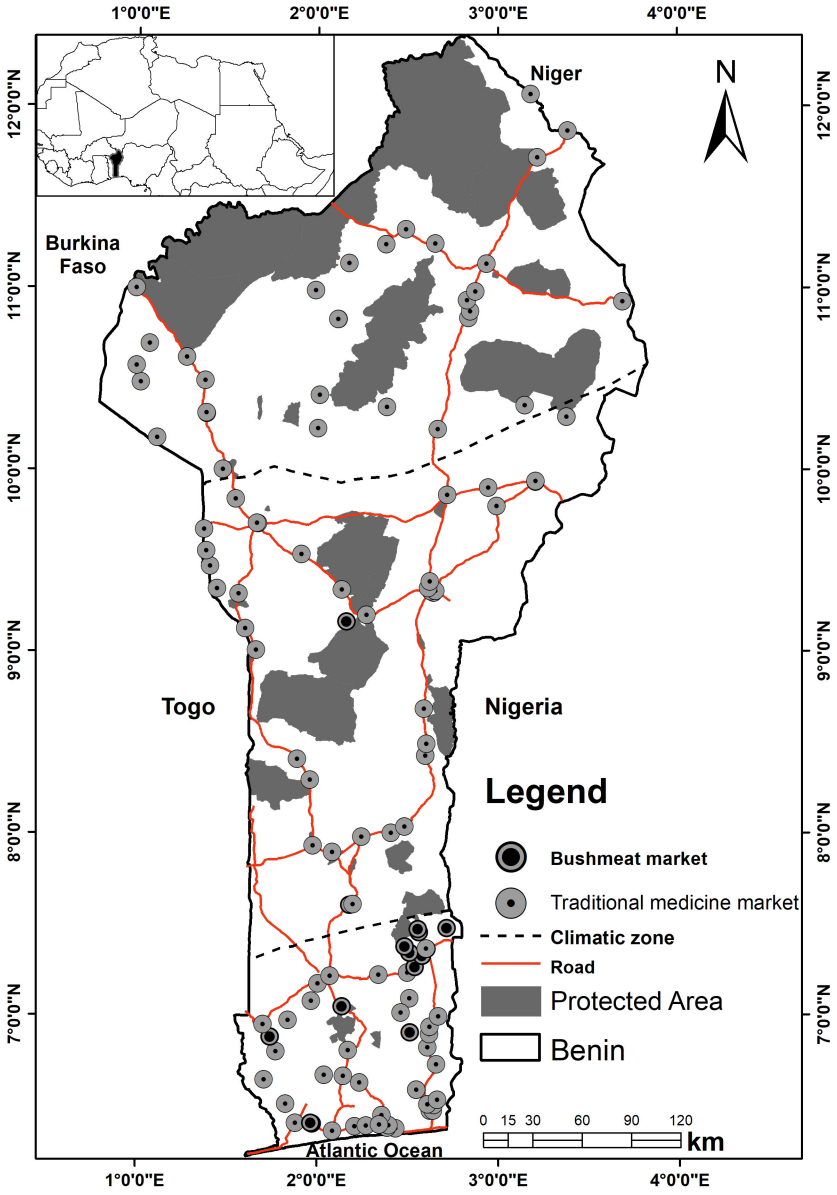

FIGURE 1
Geographic distribution of wildlife markets in Benin.

species respectively. The mammals belonged to 12 Orders, including Carnivora (27%), Rodentia (21%), Cetartiodactyla (20%) and Primates (12%). Birds belonged to 22 Orders, predominantly including Passeriformes (26%) and Accipitriformes (18%). The reptile group included only two Orders, Squamata (81%) and Testudines (19%).

At the global scale, few bird, mammal, and reptile species traded in TMM are listed as threatened on the IUCN Red List (Figure 3A). Among mammals, 75% are listed as Least Concern (LC), compared to 2%, 5%, 7% and 7% listed as Critically Endangered (CR), Endangered (EN), Vulnerable (VU) and Near Threatened (NT), respectively. A similar trend was observed for birds, for which 91% of species are Least Concern (LC), compared to 1%, 3%, 3% and 2% as Critically Endangered (CR), Endangered (EN), Vulnerable (VU) and Near Threatened (NT), respectively. Reptiles were dominated by Least Concern (LC, 69%) species, followed by vulnerable (VU, 10%), Not Evaluated (NE, 7%), Critically Endangered (CR, 3%), Endangered (EN, 3%), and (NT, 3%).

At the national scale, most birds (75%) and reptiles (68%) were unevaluated, while 61% of mammal species are evaluated as nationally threatened (CR=2%, EN=14%, VU=30% and NT=15%; Figure 3B). However, 21% of birds (CR=1%, EN=4%, VU=10% and NT=6%) and 25% of reptiles (EN=2%, VU=8% and NT=15%) were also listed as nationally threatened.

Around one third of birds (29%), mammals (34%) and reptiles (32%) are CITES-listed species, including mostly in Appendix II (28% of birds, 18% of mammals and 27% of reptiles; Figure 3C).

Referring to the national legislation, 28%, 33%, and 14% of birds, mammals and reptiles, respectively, are Integrally Protected (A), compared to 11%, 25% and 8% listed as Partially Protected (B) birds, mammals and reptiles respectively (Figure 3D).

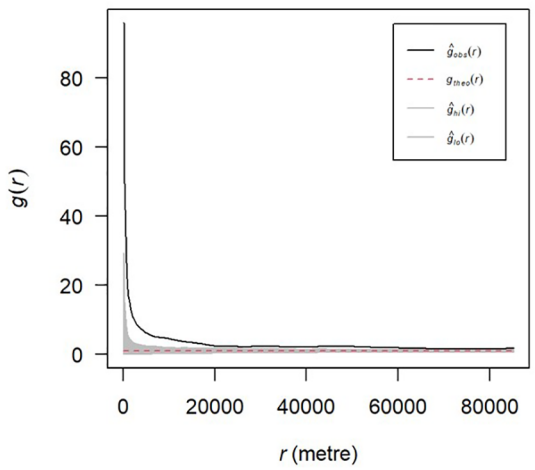

FIGURE 2
Spatial distribution pattern of wildlife markets across Benin under the null hypothesis of the Complete Spatial Randomness model (CSR). The solid black line represents the observed value of $g_{obs}(r)$ and the red dashed line indicates the theoretical value of $g_{theo}(r)$.

Scale of the wildlife trade supply chain

Traders in the TMM reported their specimens coming from across West Africa, with some rare specimens also coming from Central African range states (Figure 4). Specimens were reported as most frequently sourced from Benin and its border countries (Burkina Faso, Niger, Nigeria, Togo), though traders reported specimens coming from Cameroon, Côte d'Ivoire, Gabon, Ghana, Equatorial Guinea, Mali and Senegal (in alphabetical order) as well. Mammals were reported as more likely to be coming from countries outside of Benin, including predominantly Burkina Faso and Niger, while reptiles were most likely sourced in Benin. Frequency of citation of supplying sources varied highly significantly (X-squared = 40.655, df = 21, p-value = 0.006185) from a taxonomic group to another one.

Discussion

International recognition of wildlife trade as one of the major drivers of biodiversity loss is mainly based on international wildlife crime-based data and evidence illustrated in the UNODC's World WISE database. However, local/domestic (National) component of wildlife crime remains underrepresented and almost heedless due to the great lack of relevant data even though evidence of local trade are recorded across tropics in particular. Understanding wildlife trade in and around Benin is a big step to revealing trade throughout the West African region and others should do the same to help paint a more complete picture. The study has the merit of filling the data gap by characterizing the spatial pattern of wildlife trade and driving forces, the geographic extent of the trade and the diversity of wild animals traded in these wildlife markets in West Africa.

TABLE 1 Factors influencing the temporality (permanent *vs.* periodic) of wildlife markets in Benin.

Variables	Estimate	*p*-value
Municipal status	1.547e+00	3.12e-05 ***
Number of stalls	2.270e-01	0.007641 **
Type of market	-3.159e+00	0.000253 **
Distance to protected areas (m)	-5.020e-07	0.795485
Ecological zone	-5.413e-02	0.881888

Significance: '***' 0.001 '**' 0.01 '*' 0.05.

We identified through national georeferencing 121 wildlife markets in Benin including 15 BM and 106 TMM, with relatively high densities of TMM in all the ecological zones compared to BM, restricted to the Guineo-Congolian Zone. There is evidence that wildlife trade is among one of key economic activities widely operated in Benin as throughout the tropics (Coad et al., 2010; Brashares et al., 2011; Nielsen et al., 2014; Price, 2017; Lee et al., 2020; Ingram et al., 2021). The high density in TMM (7 times higher than BM) is inverse to the common situation in Central Africa where the wildlife trade is predominantly operated in BM (Edderai and Dame, 2006; Fa et al., 2014; Taylor et al., 2015), highlighting the use of wild animals in traditional medicine and religious practices as one of the major threat to wildlife conservation in West Africa. This uncommon dominance of TMM in Benin is likely related to the religious singularity of country (see Lin et al., 2022) due to its animal-consuming endogenous religions *Vodùn* that remains deeply-rooted among ethnic groups despite the uptake and growth development of foreign religions. Benin remains one of the countries in West Africa where the public healthcare system, mainly based on the Western model, is precarious and difficult to access for impoverished populations (Sylvest, 2013). The proliferation of traditional medicine markets is certainly driven by the strong demand for this affordable and culturally-rooted traditional medicine by impoverished populations. In 2023, the total number of TMM represents one third of the total number of pharmacies in Benin (337; https://www.abrp.bj/officine.php). The TMM, support of the cultural identity of Beninese remains resilient to the ongoing transformation of health system by the government. Undoubtedly, wildlife trade in Benin is mainly oriented towards public health and religious practices, although no national law or policy allows and encourages animal-based traditional medicine as opposed to plant-based traditional medicine. Nevertheless, the few number of BM does not mean necessary that low volumes of wild meat are extracted from forest habitats to feed this category of market for consumption, given that the main consumers of wild meat (clients of BM) remain the larger populations in urban areas (Fargeot et al., 2017; Luiselli et al., 2018). A comparative analysis of volume of wild animals extracted from the forests to supply each category of market on a daily basis could make it possible to deeply appreciate the relative amplitude of the impacts induced by each market.

The spatial analysis of wildlife markets across Benin's landscape exhibited an aggregative distribution pattern with wildlife market temporality (permanent vs. periodic) significantly explained by the type of market (P<0.001), the number of stalls in the wildlife

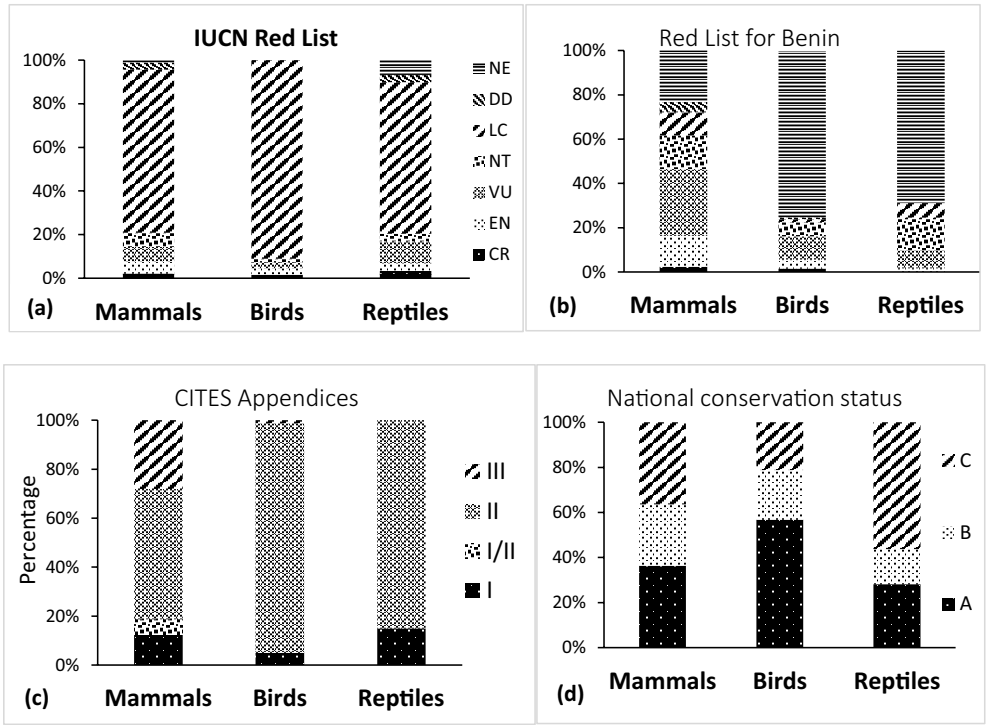

FIGURE 3
Proportion of species traded in TMM: **(A)** threatened at the global scale, **(B)** threatened at national scale, **(C)** threatened by the international trade and **(D)** protected by national law in Benin. CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; EN, Not Evaluated; A = Fully protected, B = Partially protected, C = Not protected.

markets (P<0.01) and the municipality status (P<0.001). These results mean that wildlife markets generally and permanent markets in particular mostly occurred in demographically and economically biggest municipalities (special status) and had the highest numbers of stalls. This leads to a high concentration of wildlife markets in large municipalities to the detriment of smaller ones from southern to northern Benin. These findings corroborate the fundamental law of supply and demand in economy (here, increasing consumers' demand correspond to growing number of wild specimens stalls) but also support previous studies that pointed out the economic chain related to the wildlife trade and its importance as an income source for local people (Fa et al., 2014; Nielsen et al., 2014; Price, 2017; Lee et al., 2020; Ingram et al., 2021). The Guineo-Congolian ecological zone where the higher density of wildlife markets has been recorded overlaps the southern Benin that encompasses most of larger cities (including both economic and administrative capitals) and more than 50% of the human population (INSAE, 2013). These results are in line with previous studies that underpinned the strong incentives of large urban human populations on wildlife harvesting in West and Central Africa (Fargeot et al., 2017; Luiselli et al., 2018). They support aforementioned demographic and economic factors underlying the spatial distribution and temporality of markets across Benin.

TMM-based surveys revealed a high species richness in birds (268 species), mammals (96 species) and reptiles (59 species) with species richness in birds 4 and 6 times higher than mammals and reptiles respectively. Contrary to previous studies that pointed out mammals as the most affected taxonomic group by the wildlife trade (Whiting et al., 2011; Petrozzi et al., 2016; Gbogbo and Daniels, 2019), birds were dominant taxonomic group in terms of the number of species on TMM in Benin. Species recorded on TMM represents 20% (268/1371), 14% (96/663) and 10% (59/601) of bird, mammal and reptile richness respectively in West and Central Africa (Mallon et al., 2015). Referring to the country-level data (Benin), the diversity recorded on TMM represents 45% (268/590), 61% (96/157) and 58% (59/103) of bird, mammal and reptile richness respectively (Sinsin and Kampmann, 2010; Dowset-Lemaire and Dowset, 2019). The trade in wild animals on TMM affects relatively more species in Benin than South Africa (53 bird species, 60 mammal species and 33 reptiles; Whiting et al., 2011); Ghana (15 bird species, 16 mammal species and 8 reptiles; Gbogbo and Daniels, 2019) and in Togo (2 bird species, 22 mammal species and 2 reptiles; Sonhaye-Ouyé et al., 2022). However, a single sale site was surveyed in South Africa whereas surveys were restricted to the eight largest TMM in Accra (Ghana), contrary to our study that investigated a large area including several cities and 10 TMM. A comparison of our findings with those of BM in West and Central Africa shows a high species richness of TMM in Benin compared to BM from Cameroon, Ghana, Nigeria, Equatorial Guniea and Democratic Republic of Congo together (14 bird species, 91 mammal species and 19 reptiles; Petrozzi et al., 2016). Another relatively lower species richness was obtained for surveys conducted on 89 BM in Nigeria and Cameroon (Fa et al., 2014). The high numbers of species than those we obtained were reported for birds

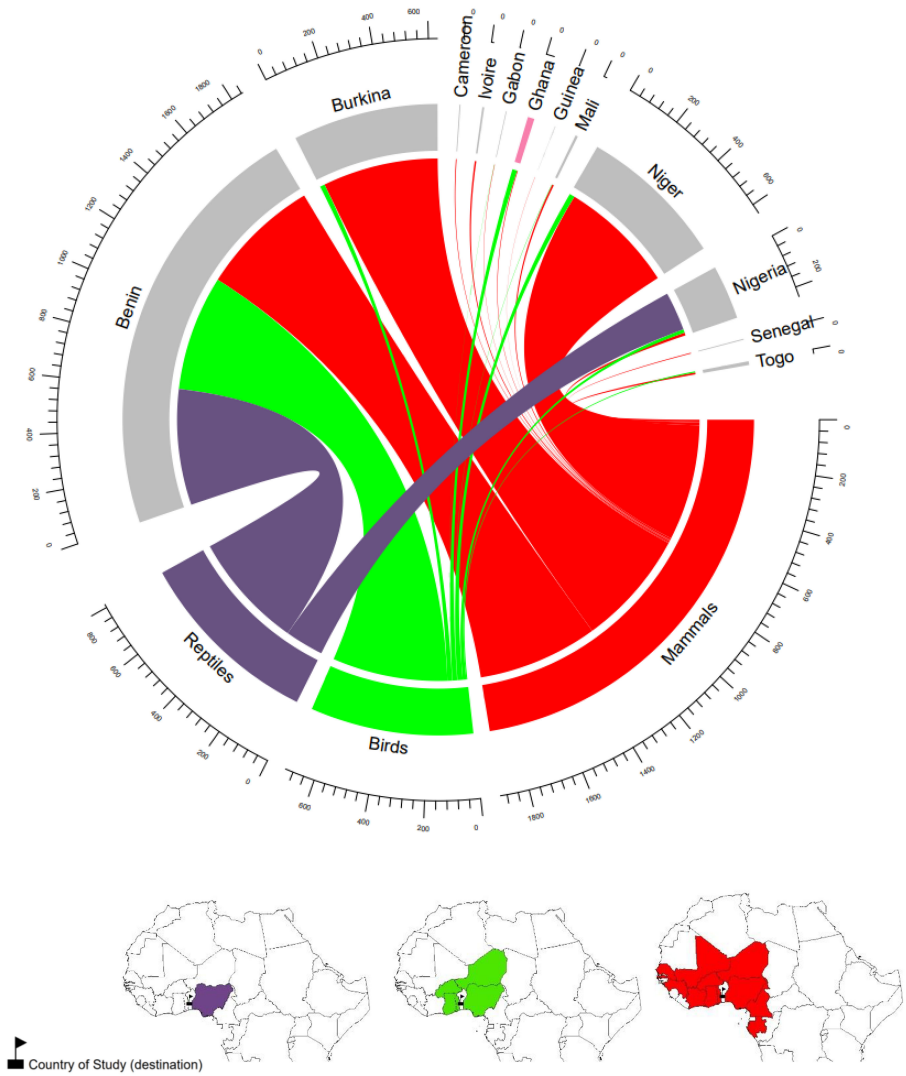

FIGURE 4
Diversity of supplying sources in wildlife of the traditional medicine markets in Benin. Ivoire= Côte d'Ivoire, Guinea = Equatorial Guinea, Burkina = Burkina Faso. The color on the maps represent each taxonomic group of the circular layout.

through systematic literature reviews involving 25 African countries (354 bird species; Williams et al., 2014), and 10 West and Central countries (354 bird species; Petrozzi, 2018). Moshoeu (2017) estimated a relatively high species richness in reptiles (101 species) across 30 African countries. Our study supports the important contribution of TMM in Benin to the regional estimations of the trade in bird species for the traditional medicine, counting for more than 50% of bird species (Petrozzi, 2018). The same trends could be observed for other non-focal taxonomic groups.

Our surveys ranked Carnivora (27%), Rodentia (21%), Cetartiodactyla (20%) and Primates (12%) as the main mammal orders available on TMM; Passeriformes (26%) and Accipitriformes (18%) for birds and the Squamata (81%) as the most represented order for reptiles. For mammals and birds, our findings are in line with previous studies that had already reported dominance of these different orders in the wildlife trade across West and Central Africa (Djagoun et al., 2013; Williams et al., 2014; Petrozzi, 2018; Djagoun et al., 2023) but across Africa for reptiles (Moshoeu, 2017). We identified during interviews, Charadriiformes (03 species) and Psittaciformes (04 species) that had only been found on TMM in Benin (see Petrozzi, 2018).

On TMM occurs all the conservation profiles even if the high numbers of non-threatened (*NT*, *LC*, and *DD*) and Not Evaluated (*NE*) species on the IUCN Red List of Threatened Species and on the Red List for Benin were reported for all the focal taxonomic groups. Some comparisons based on the number of threatened species in Benin according to the IUCN (2020) shows that all the threatened birds (12/12), reptiles (7/7) and almost all the high concern mammal species (13/16) are affected by the local trade on TMM. These findings are a further evidence of harmful impacts of wildlife trade on local and regional biodiversity. Similar results were reported for all the surveys relative to wildlife trade across Africa (Djagoun et al., 2013; Williams et al., 2014; Petrozzi et al., 2016; Moshoeu, 2017; Petrozzi, 2018; Sackey et al., 2023; Djagoun et al., 2023). The large spectrum of species (a total of 426 species for both

three groups) affected by the trade including many large-bodied seed dispersers (i.e primates, antelopes, bats etc.) and high concern species would lead to severe defaunation, a decreasing of the carbon balance and consequently will emphasize climate change (see Bello et al., 2015).

Our inventory on TMM revealed that one third of recorded species, were CITES-listed species including a high number of species listed on the Appendix II. Among CITES-listed species, four mammals (*Acinonyx jubatus*, *Panthera pardus*, *Phataginus tricuspis*, *Gorilla gorilla*) and three reptiles (*Boa constrictor*, *Chelonia mydas*, *Lepidochelys olivacea*) were listed on the Appendix I. The trade affects not only the IUCN high concern species but also some species threatened by international trade (Williams et al., 2014; Petrozzi et al., 2016; Moshoeu, 2017; Petrozzi, 2018; Djagoun et al., 2023). In West Africa, 99 mammals and 113 birds were listed on the CITES Appendices (Cormier-Salem et al., 2018) whereas 44 out of 101 reptiles reported across Africa were listed on Appendix I or II (Moshoeu, 2017). Using the above-mentioned reference frameworks, 69% (79/113) of bird species, 32% (32/99) of mammal species and 45% of (20/44) reptiles species listed on CITES Appendices were openly sold on TMM. Out of species under international reference frameworks (IUCN Red List of Threatened Species and CITES Appendices), it was recorded on TMM some fully protected species (75 bird species, 32 mammal species and 8 reptile species) by the National legislations ((see, Supplementary Tables S1–S3, Supplementary information). These findings underpin the ineffectiveness of law enforcement at national level and call for urgent regulation of wildlife trade, in particular on TMM. It is quite clear that there is an illegal dimension of the local trade.

Out of the distribution pattern of wildlife markets, the diversity of bird, mammal and reptile species traded on TMM and their conservation profiles at national and international scales, our investigations delineated a regional trade including all the countries of the West African Economic and Monetary Union (WAEMU) except (Guinea-Bissau) and 12/15 of the Economic Community of West African States (ECOWAS). This means that almost all the West African countries supply TMM in wild animals in Benin. These results support the long-distance trade underpinned recently in the Dahomey Gap (Zanvo et al., 2022). The trade in wildlife follows probably the same routes as the goods between the states of WAEMU and ECOWAS that established strong economic ties several decades ago. This raises the problem of porous borders and weak enforcement at borders, which facilitate this regional trafficking. According to IUCN (2020), it occurs 7 and 12 threatened reptile and bird species respectively in Benin, but our inventory identified on TMM 8 and 19 threatened reptile and bird species respectively on the IUCN Red List (Supplementary Tables S2, S3, Supplementary Material). Moreover, some species recorded on TMM were non-native species to Benin but native species to the West and Central Africa (Supplementary Tables S1–S3; Supplementary Material). There is no doubt that TMM in Benin are supplied in wildlife from the states belonging to WAEMU and ECOWAS. Whatever the taxonomic group considered, the most cited supplying sources were Benin and its border countries (Burkina Faso, Niger, Nigeria). These results show a wildlife trade mainly centered on the available wildlife resources in Benin and its neighboring counties (Burkina Faso, Niger and Nigeria) with some remote connection with Western and Central Africa countries. LEK-based surveys revealed a lower diversity of supplying sources in reptiles contrary to mammals and birds. Given Benin is recognized as one of most prolific reptile-exporting country in the world (Harwood, 2003; Auliya et al., 2016), may be the availability of sizeable populations of reptiles could explain the limited number supplying sources contrary to mammals and birds. Moreover, Benin has several captive breeding farms across the country on which large quantities of reptiles (turtles, python, lizards) are bred every year (SZ, pers. obs.). However, the fact that one fourth of reptile specimens sold in markets come from Nigeria, points out that this country participates to the international trafficking via Benin. In view of Benin's place in the illegal wildlife (native and non-native) trade at regional level, the challenges linked to securing borders, the weakness of law enforcement in the country and the growing dynamic of cases of seizures of animal specimens from Nigeria in particular (SZ, pers. obs.), we hypothesize that Benin is probably becoming a hub of international illegal wildlife trafficking. An in-depth study of the wildlife trade chain involving a wide range of actors (TMM and BM vendors, consumers, forest officers, customs officers and border populations, etc.) and national seizure data is needed to shed light on the links between local/regional trade and international trafficking, the extra-continental drivers and Benin's level of involvement for informed interventions against wildlife crime.

Implications for conservation

Sustainable development, the fight against accelerating biodiversity loss and degradation, as well as climate change inexorably requires rational management of biodiversity at the level of each country and the implementation of more structured and inclusive strategies at regional and international level against the illegal trade in wildlife. This can only be effective in a context where each nation has up-to-date and reliable information. Our study has the merit of deciphering wildlife trade in its current form in West Africa. Data relating to the number of markets, the spatial configuration of markets, their spatial temporality, then their weight (number of stalls) and the factors influencing this temporality constitute an important source of information for developing a national strategy to regulate the local wildlife trade and combat the illegal trade. These data could be used for spatial prioritization of actions against the illegal wildlife trade. Data on species of major conservation concern, cross-referenced with the occurrence areas of the different species in Benin, will make it possible to identify the habitats on which it will be necessary to concentrate more conservation efforts to avoid local extinction of these species. Our investigations revealed the presence in the stalls of TMM some species fully protected by national legislation. This evidence should raise awareness of public forest services for rigorous law enforcement, even in TMM which carry the cultural identity of Beninese and which until now have remained free of all regulations. In addition, religious leaders/community need to be actively brought into the different conservation efforts using a top-down approach. Using the

species diversity obtained from our investigations, the Beninese Government could update the list of protected species in Benin. Thus, certain species, given the level of threat and the scientific data available on their abundance, could change category. Our results clearly suggest that the sources of animals that supply TMM go beyond Beninese borders, and it occurs a regional wildlife trade violating the regional commitments to combat wildlife trafficking such as West African Strategy for Combatting Wildlife Crime. Our data could help update the regional strategy. These data will allow a targeted fight against animal trafficking and are of paramount importance for planning a regional fight against wildlife crimes through transnational cooperation.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The studies involving humans were approved by the Research Ethics Committee of the University of Abomey-Calavi (#4613). The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their informed consent to participate in this study.

Author contributions

SZ: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Software, Visualization, Writing – original draft. SD: Data curation, Formal analysis, Funding acquisition, Investigation, Visualization, Writing – original draft. JA: Data curation, Investigation, Methodology, Visualization, Writing – original draft. AA: Software, Validation, Visualization, Writing – review & editing. BD: Supervision, Validation, Writing – review & editing. ES: Conceptualization, Supervision, Validation, Writing – review & editing. BS: Conceptualization, Project administration, Supervision, Validation, Writing – review & editing. CD: Software, Supervision, Validation, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1481791/full#supplementary-material

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