Pre- and post-Ebola outbreak trends in wild meat trade in West Africa

Stephan M. Funk [a], Julia E. Fa [b,c,*], Stephanie N. Ajong [d], Edem A. Eniang [e], Daniele Dendi [f,g,h], Massimiliano Di Vittorio [i], Fabio Petrozzi [j], NioKing Amadi [g], Godfrey C. Akani [g], Luca Luiselli [f,g,h]

[a] *NatureHeritage, Jersey, Channel Islands, UK*
[b] *Department of Natural Sciences, School of Science and the Environment, Manchester Metropolitan University, Manchester M1 5GD, UK*
[c] *Center for International Forestry Research (CIFOR), CIFOR Headquarters, Bogor 16115, Indonesia*
[d] *Department of Fisheries, Lagos State University, Ojo, Lagos, Nigeria*
[e] *Department of Forestry and Wildlife, University of Uyo, Akwa-Ibom State, Nigeria*
[f] *Institute for Development, Ecology, Conservation and Cooperation, Rome, Italy*
[g] *Department of Applied and Environmental Biology, Rivers State University of Science and Technology, Port Harcourt, Nigeria*
[h] *Département de Zoologie et Biologie Animale, Faculté des Sciences, Université de Lomé, Lomé, Togo*
[i] *Ecologia Applicata Italia, Termini Imerese, Palermo, Italy*
[j] *Ecolobby, Rome, Italy*

ARTICLE INFO

Keywords:
Wild meat
Nigeria
Markets
Mammals
Reptiles
Ebola virus disease (EVD)

ABSTRACT

Ebola virus disease, EVD, has been linked with wild meat. In Nigeria, strict restrictions on wild meat sales were applied after the first case in July 2014. We quantified wild meat trade in nine markets in southern Nigeria, during Oct. 2010 – Dec. 2019, and undertook consumer interviews during 2018–2019. Wild meat sales fell to low levels between during EVD (Jul. - Oct. 2014), after which Nigeria was declared Ebola-free. Prior to EVD (2012–2014), reptile carcass numbers declined markedly, collapsed during EVD, but rebounded immediately post-EVD until 2017 to values exceeding pre-EVD (especially true for turtles and tortoises). Reptile consumption increased as mammal numbers declined. After 2017, reptile numbers fell and remained low until the end of the study, indicating population collapses and depletion. Fruit bats and primates did not recover after EVD, but ungulates, rodents and carnivores increased significantly after EVD though never reached pre-EVD levels. Interviews revealed strong rural versus urban and age-specific differences regarding wild meat consumption and attitudes. Most people worried about Ebola and more than half of interviewees agreed that wild meat poses a transmission risk. Except urban males, over-60-year olds were least informed about the Ebola risk of wild meat, indicating that any future behavioural change campaign should focus on the younger age classes. Unlike other studies, our research clearly shows that changes in purchasing behaviour of consumers and education campaigns were effective in reducing the trade of bats and primates, animal groups likely to be implicated in the transmission of Ebola.

1. Introduction

Ebola virus disease (EVD), is a rare but severe, often fatal illness in humans. Caused by a number of related filoviruses, *Bundibugyo ebolavirus*, *Sudan ebolavirus*, and *Zaire ebolavirus*, overall case fatalities of 25%, 50% and 80%, have been reported for each, respectively (Malvy et al., 2019). A total of 28 EVD outbreaks have been recorded since 1976 (Centers for Disease Control and Prevention, 2020), the most severe in terms of number of deaths from 2014 to 2016 in multiple West African countries. As many as 11,325 deaths (Centers for Disease Control and Prevention, 2020) were documented, 11,310 of which were only in Guinea, Liberia and Sierra Leone (WHO, 2016). The butchering and manipulation of infected animals for their meat has been reportedly implicated in the virus spill-over. All five human EVD outbreaks during 2001–2003 in the forest zone between Gabon and Republic of Congo began after humans handled gorillas, chimpanzee, and duiker carcasses infected with the virus (Rouquet et al., 2005). The first human victim of an EVD outbreak in the Democratic Republic of the Congo in 2007 died

* Corresponding author at: Department of Natural Sciences, School of Science and the Environment, Manchester Metropolitan University, Manchester M1 5GD, UK.
E-mail addresses: jfa949@gmail.com (J.E. Fa), d.dendi@ideccngo.org (D. Dendi), king.amadi@ust.edu.ng (N. Amadi), l.luiselli@ideccngo.org (L. Luiselli).

after direct exposure to a fruit bat after purchasing one in a market (Leroy et al., 2009; Mann et al., 2015). In addition, circumstantial evidence points to the source of the West African 2014–2016 outbreak to direct contact with wild fruit bats by humans (Mann et al., 2015).

Because of the severity of EVD and its link with wild meat, severely affected Western African countries (Guinea, Liberia and Sierra Leone) but also neighbouring countries such as Ivory Coast, Togo and Nigeria imposed strict restrictions on the sale of wild meat and conducted information campaigns to discourage consumption after EVD arrived in each of these countries (Akani et al., 2015; Alpha and Figuié, 2016; Dindé et al., 2017; Duonamou et al., 2020). In Nigeria, immediately after the onset of the outbreak the Ebola Emergency Operations Center (EEOC) was established with a focus on establish an EVD treatment centre with laboratory support and health surveillance of travellers (Vaz et al., 2016). Its social mobilization unit created general awareness with a focus on community members around the homes of EVD case patients. It also extended to the general population by informing community representatives, schoolteachers, and healthcare workers through talks and information campaigns in television, schools, churches, through general distribution of communication materials, (such as hand bills, posters and banners) and through establishing an Ebola alert call centre with toll-free lines. However, increased policing of wild meat markets was not explicitly listed as an activity of the EEOC (Vaz et al., 2016).

Immediately after the first case in Nigeria in July 2014 (due to an airplane passenger coming from Liberia and landing in Lagos airport), surveys undertaken in nine wild meat markets in southern Nigeria indicated that monkeys and fruit bats nearly disappeared whilst other wild meat sales dropped significantly (Akani et al., 2015). In two other Nigerian studies, the numbers of wild meat buyers in markets also dropped significantly (Oyediran et al., 2015; Ozioko et al., 2018). In Côte d'Ivoire, the proportion of households consuming wild meat at least once per week decreased from 59.2% to 19.8% (Dindé et al., 2017). Similarly, in Liberia Ordaz-Németh et al. (2017) found an overall decrease in wild meat consumption. Thus, it appeared very clear that wild meat consumption decreased considerably during the West African Ebola crisis.

In Guinea, the "epicentre" of the EVD outbreak, awareness campaigns led to a significant reduction in the presence of wild meat on market stalls in urban areas, with bats and chimpanzees reportedly consumed significantly less often than before the EVD epidemic; not the case for any of the other traded faunal groups (Duonamou et al., 2020). However, the ban on wild meat hunting has had a limited effect. Apart from bats and primates for which consumers remain afraid, wild meat dishes were easily found in small local restaurants in West Africa (Guinea, Sierra Leone and Liberia; Alpha and Figuié, 2016). In Côte d'Ivoire, Dindé et al. (2017) argued that the drop in wild meat consumption was not due to the awareness of the health threat from EVD but to the repressive measures taken by the government in case of non-compliance with the law, pushing the wild meat trade into illegality. Despite bans and public awareness-raising campaigns, the majority of respondents in rural areas did not believe that wildlife could act as vectors of EVD (Duonamou et al., 2020). In Ghana, perceptions of disease risk were generally low, with high levels of uncertainty (Lawson et al., 2017) whereas in Sierra Leone people felt that the ban and the education campaigns contradicted their own lifetime experience of low risk due to the eating of wild meat (Bonwitt et al., 2018). In another study in Benin City, Nigeria, 63.5% of market traders believed that the virus exists and the link between the virus and wild meat consumption whilst some consumers, hunters and traders saw it as conspiracy by government to discourage wild meat trade and hunting (Ogoanah and Oboh, 2017). Whilst prices dropped during the EVD epidemics, half of market traders reported no change, and about a quarter reported increases with the remainder indicating a decrease in sales volume. According to some studies, wild meat prices returned to pre-EVD levels immediately after the country was declared free of Ebola (Ogoanah and Oboh, 2017). In a different Nigerian market of the Nsukka Agricultural Zone in Enugu State, Onyekuru et al. (2018) reported that wild meat sales and consumption dropped during the EVD epidemics but similar to Benin City returned to previous levels afterwards. The research conducted in Benin City and the Nsukka Agricultural Zone were short-term studies from December 2014 and April 2015 (i.e., shortly after Nigeria was declared free of EVD) and in 2016, respectively (Ogoanah and Oboh, 2017; Onyekuru et al., 2018).

Whilst most of the reported studies on wild meat sales in markets immediately pre- and post the EVD outbreak in West Africa indicate an effect, no information has been published on the longer-term effects. Understanding wild meat consumer responses to zoonotic disease outbreaks may help guide policy interventions. Here we monitor the impact of EVD on the trade of wild meat in markets in southern Nigeria for a period of six years after the outbreak where we previously reported that the sales of wild meat crashed immediately after the first Nigerian EVD case in 2014 (Akani et al., 2015). To understand the prevailing attitudes of consumers to wild meat according to gender, rural/urban living and age class, we also conducted structured interviews. In this paper we investigated whether Nigerian consumers restricted their wild meat consumption after the country was declared free of EVD or returned to pre-epidemic levels immediately after. We also investigated the effects of the timespan passed since the EVD period on the consumption patterns, as well as the effects of the site (market individuality) and of the season (dry versus wet) on the consumption patterns for various groups of terrestrial vertebrates.

2. Materials and methods

2.1. Study area

We monitored nine main wild meat markets along the main roads and the courses of the principal rivers and urban centres in the Niger Delta, southern Nigeria (Mosogar, Patani, Oredo, Imo River Bridge, Omagwa, Akabuka, Ahoada, Mbiama and Eket Bridge) (Fig. 1). Each of these wild meat markets are served by distinct forest blocks of the Niger Delta region. The area is densely populated and the wild meat trade has been traditionally an important source of food and income (Fa et al., 2006; Luiselli et al., 2013). The study area is heavily populated with hundreds of villages interspersed by patches of deltaic moist and flooded forests and cultivated lands (mainly cassava, plantains, oil palms). The climate of the study area is tropical, with well-delineated dry (from November to March) and wet (from April to October) seasons.

2.2. Sampling design and market data collection

We sampled wild meat entering the sampled markets between Oct. 2010 and Dec. 2019, i.e., before and after EVD. The first case of Ebola in Nigeria was on 20 July 2014 leading to the death of seven people; the WHO declared the country free of Ebola on 20 Oct. 2014 (WHO, 2014).

Wild meat was sent to the markets by hunters who were active in the Niger Delta (Akani et al., 1998). The markets contained around 20–30 counters each on which animal carcasses were laid out for customers to view the merchandise. During each survey day, we counted the total number of carcasses displayed by sellers very early in the morning (i.e., from 06 h00 to 08 h00) i.e., when carcasses arrived at the markets and before they were "dressed", and the selling started. In this way, we were confident we could count nearly all carcasses that were for sale on each day. We did not survey the same markets on consecutive days but at regular time intervals (2 = 4 times a month but mostly once every 10 days), so we are not sure whether the unsold carcasses were kept stored for display the next day. However, this is unlikely except for animals that were sold alive (turtles and tortoises, and occasionally monitor lizards and crocodiles). After the EVD outbreak in 2014, markets were surveyed monthly, but survey intensity before the EVD outbreak was less intense (Fig. 2). The number of carcasses was averaged across all surveyed markets as these were similar size in terms of daily numbers of traded

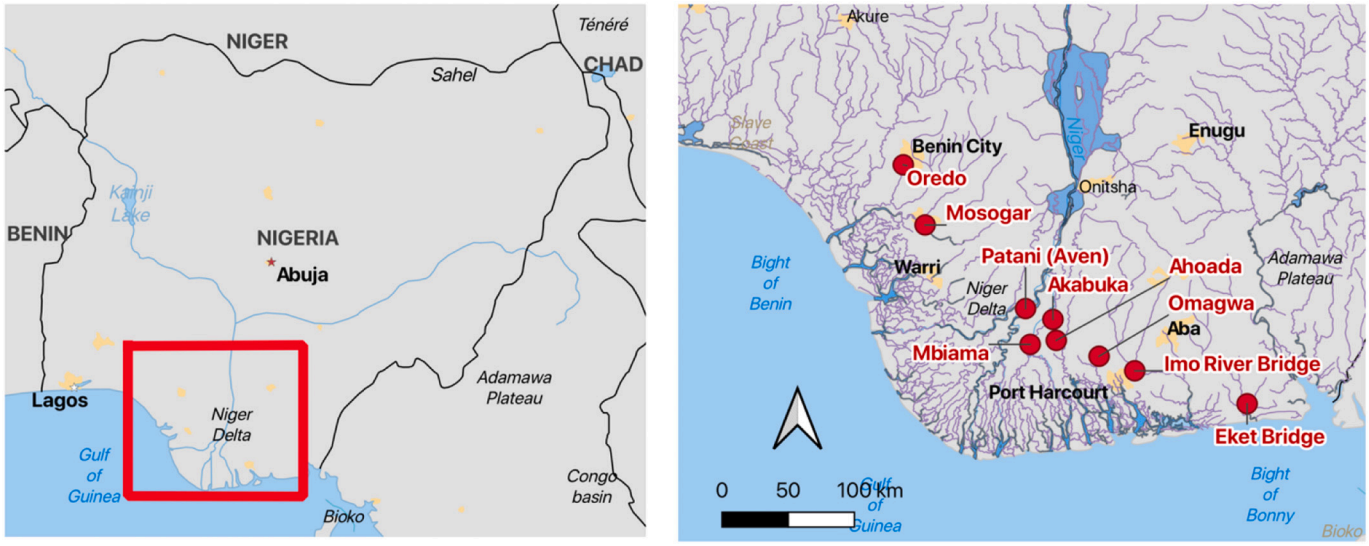

Fig. 1. Map of Nigeria showing the nine market sites surveyed during the present study. Source: public domain map data from Open Street Map, diva-gis (diva-gis.org) and Natural Earth (www.naturalearthdata.com).

carcasses (Akani et al., 2015).

Many market traders were personally known to the surveyors for a long time, resulting in mutual trust. Although we cannot unequivocally demonstrate that the level of trust remained the same after the government's ban on sales, we believe that there was no change especially as the enforcement of the ban was low (see discussion). We therefore suggest that the numbers of carcasses counted are representative of the actual traded volume (Akani et al., 2015). Thus, given this and the early morning counts we performed, we were confident that nearly all carcasses were recorded during each survey day.

2.3. Consumer interviews

Structured interviews with customers were conducted in the various studied markets. Participants were selected randomly (between 10 h30 and 12 h00 on some survey days) during 2018–2019. We did not interview minors of less than 18 years, and we kept anonymity to the interviewees for privacy reasons. All interviewees were notified that their identity would be kept anonymous. To avoid re-interviewing the same persons, before starting their interview we always asked them whether they had been interviewed before for our project. We openly informed each interviewee about the scope of our study before applying the questionnaire, and their gender was recorded. Rural versus urban origin of the interviewees was attributed on the basis of their actual residence. We considered "urban" all interviewees with residence in a town exceeding 15,000 people according to the 2006 Population Census of the Federal Republic of Nigeria. The questions were: What is your age? Where do you live? Do you like wild meat? Are you worried because of Ebola? Do you still eat wild meat after Ebola? Do you agree that wild meat carries Ebola? What won't you eat again because of Ebola, if anything?

2.4. Statistical analyses

Because of the nature of the data as time series, the data are statistically not independent from each other. We thus used the Mann-Kendall test for monotonic trend in the time series after the EVD outbreak from 2016 to 2019, as implemented in the R package "randtests" (Caeiro and Mateus, 2014; Mateus and Caeiro, 2015). For each of the survey questions, we tested difference in rural versus urban interviewees and males versus females in each age group (18–25 years, 26–45 years, 46–60 years, older than 60 years) using a Fisher's exact test as implemented in R (R Foundation for Statistical Computing, 2018).

3. Results

3.1. Animal traded volumes: trends by taxonomic groups

After Ebola reached Nigeria in July 2014, all wild meat sales went down to very low levels in the period till October 2014, when Nigeria was declared free of Ebola. The numbers of sales of all animal groups except reptiles remained low until the end of 2016 (Fig. 2, Table 1). For all animal groups except reptiles, mean sales in 2016 were lower than between 2017 and 2019 (Table 1). Whilst there was no evident trend in market sales pre-EVD for all animal groups except reptiles, a marked decline in reptile carcasses was observed between 2012 and 2014, prior to the EVD outbreak. Trade volume collapsed in 2014, but in 2016 volume exceeded, on average, three times more than the mean volume in 2013/4 pre-EVD (Fig. 2, Table 1). There was a decline in number of reptiles traded in the last two sampled months of 2016, after which numbers were comparable to immediately before EVD and did not change until the end of the study. Average traded numbers ranged between 0.4 and 0.8 for snakes, crocodiles, *Varanus ornatus* and *Kinixys* sp. but were with 4.8 about fivefold as high for turtles from 2017 to 2019 (Table 1). The negative trend in sales volume between 2016 and 2019 was significant for reptiles jointly and for snakes, turtles, crocodiles, *Varanus ornatus* and *Kinixys* sp. separately (Mann-Kendall statistics, Table 1, Fig. 3). Fruit bats and primates did not recover after the end of EVD for the survey period from January 2016 to December 2019 but an upward trend was significant for bush pigs, carnivores, rodents and ungulates for the same time period after the end of EVD (Mann-Kendall statistics, Table 1). In each of these cases, the upward trend did not reach pre-EVD levels (Fig. 2).

3.2. Interview results

A total of 570 interviews were conducted, 326 with urban and 244 with rural people. More men (n = 354) than women (n = 216) participated in these. Age classes were about equally represented (age 18–25, n = 110; age 26–45, n = 147; age 46–60: n = 190; age > 60, n = 123). The number of interviews per market ranged from 54 to 121 (mean = 95; Standard Deviation = 22.3, median = 100), but was too small for intermarket analysis by sex and age group. Except for giant rats, rural respondents stated less often than urban respondents that they will not

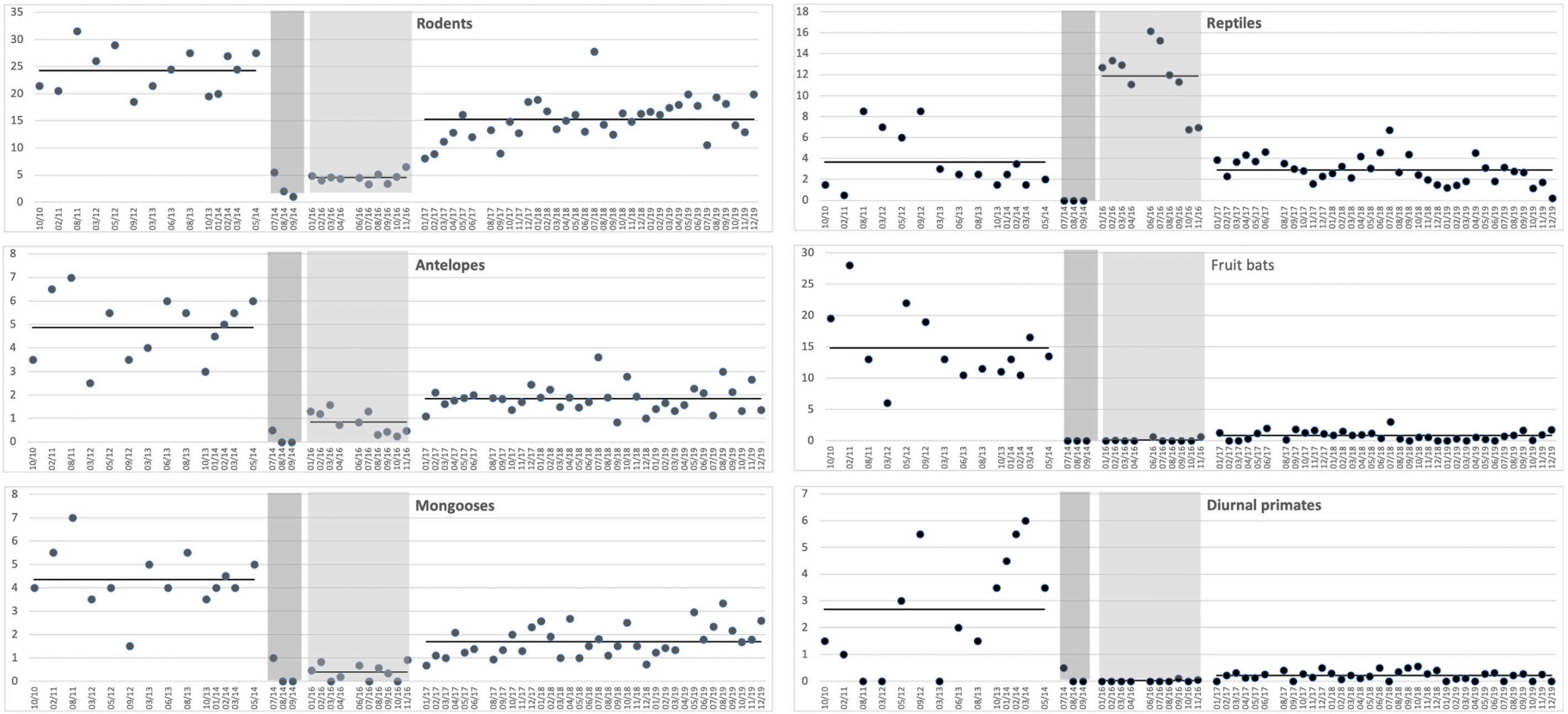

Fig. 2. Trend in the monthly mean numbers of traded carcasses in nine bushmeat markets in southern Nigeria, before and after Ebola outbreak in June 2014. The 62 monthly surveys utilized on average 14 visits (min = 5, max = 23) of the 9 markets. The months with Ebola, July to September 2014, are marked in dark grey. We did not sample in 2015. Surveys for 2016, when Ebola was absent from Nigeria but still present in the three most affected countries (Guinea, Liberia, Sierra Leone; Centres for Disease Control and Prevention CDC, 2016) are marked in light grey. Amongst primates, only diurnal species were registered as they are used for meat, whereas nocturnal species such as galagos, which are used for pharmacopeia purposes, were not included.

Table 1
Summary of mean monthly meat sales before and after ebola virus disease, EVD, and trend of monthly meat sales after EVD. The hypothesis of "no trend" was tested against the alternative hypothesis H_a by Mann-Kendall statistics.

	Before EVD		After EVD					
	Mean meat sales 2010 - May 2014	Survey months n	Mean meat sales 2016	Mean meat sales 2017–9	Survey months n	Trend H_a	Mann-Kendall statistic	p-value
Antelopes	4.9	14	0.8	1.8	45	Upward	2.739	0.003
Bush pigs	–	0	0.6	0.9	43	Upward	2	0.023
Carnivores	4.4	14	0.4	1.7	44	Upward	4.976	<0.001
Fruit bats	14.8	14	0.1	0.8	45	Upward	0.548	0.29
Monkeys	2.7	14	0.0	0.2	45	Upward	0.841	0.2
Reptiles	3.6	14	2.1	0.8	45	Downward	−5.6	<0.001
Crocodiles	–	0	1.8	0.4	45	Downward	−5.204	<0.001
Kinixys sp.	–	0	4.2	0.6	45	Downward	−4.383	<0.001
Snakes	–	0	2.0	0.7	45	Downward	−5.556	<0.001
Turtles	–	0	9.3	4.6	45	Downward	−1.82	0.034
Varanus ornatus	–	0	3.1	0.8	45	Downward	−6.143	<0.001
Rodents	24.2	14	4.5	15.3	45	Upward	5.83	<0.001

eat specific animals again (Fig. 4). Over 80% of rural and urban respondents stated that they will not eat bats and monkeys again (Fig. 4), reflecting the lack of market sales of these two groups (Fig. 2). The difference between rural and urban interviewees was not significant for bats but significant for monkeys (Fig. 4). For carnivores and giant rats, the percentage was between 20 and 30% with no significant differences between rural and urban people. Grasscutters were mentioned as likely to be eaten by all rural people and by 95% of urban people with the difference being significant. In total, 22% of rural people and 11% of urban people answered that they would not change their eating habits, but the difference was not significant.

A strong age difference was observed regarding whether respondents like wild meat (Fig. 5). Few (6%) young people aged 25 or less did like wild meat irrespective of place of living. More (31%) people of the age class 26–45 liked it whereby significantly more rural people liked it than urban people. The same urban versus rural significant difference was seen for 46 to 60-year-olds and the older than 60 years, with 62% of the former and 88% of the latter liking wild meat. Gender differences in replies were significant only for the over-60-year-olds. The same trend over age was seen for the question "do you still eat wild meat after Ebola?" with 0%, 3%, 31% and 78% of respondents with increasing age classes still eating wild meat. For the two older age classes, significantly more women ate wild meat than men.

No urban/rural difference or gender difference in any age class was observed for the question whether people are worried about Ebola. Percentages were very high over all ages although a decrease in worry was observed with increasing age (98%, 95%, 90% and 78%, respectively). The percentages of people that agrees that wild meat might contain Ebola was 75%, 86%, 72% and 39%, respectively, over age classes. In each age class, urban people agreed significantly more often than rural people. Only for the over-60-year-olds, the gender difference was significant with men agreeing more often than women.

4. Discussion

The 2014 EVD outbreak in West Africa, which persisted for more than 2 years was the longest, largest, deadliest, and most complex epidemic of its kind in history (United Nations Development Group 2015). Despite the fact that the epicentre of the outbreak was around south-eastern Guinea, Sierra Leone and Liberia, bans on the consumption and sale of wild meat was imposed in other West African countries as far as Nigeria (Dindé et al., 2017; Bonwitt et al., 2018; Onyekuru et al., 2020). In all countries where the ban was enforced significant declines in sales and consumption of wild meat have been recorded (see Onyekuru et al., 2020 for south-east Nigeria). In this study, we monitored the sale of wild meat in nine markets for a constant period of five years before, during and after the EVD outbreak in the Niger Delta, Nigeria. As in other studies, we showed that wild meat sales dropped dramatically but we also revealed that trends in sales volume differed by species and animal groups. We show clearly that the bats and primates, the two animal orders which have been subject to education and information campaigns suggesting these are responsible for the Ebola transmission, never recovered from the significant drop of sales after EVD. Sales of animals from both orders stayed near zero up to the end of 2019. Mongooses, antelopes and rodent sales stayed low up to the end of 2016 when EVD ended across the whole West African region. Subsequently, sales increased for these three mammal groups but never reached pre-EVD levels. The same distinction of bats and primates versus rodents and carnivores where a very high percentage of interviewees (over 80%) avoided the first two groups but not the other two groups (0% to 30%). The recovery of antelope sales may be considered surprising since duikers have been directly implicated alongside primates during the 2001–2003 EVD outbreaks in Gabon and Republic of Congo (Rouquet et al., 2005). However, the government propaganda against Ebola in Nigeria did not openly deterred people from antelope consumption, and so it may be possible that most consumers were simply uninformed about the role have played by antelopes in Ebola spread in Gabon and Republic of Congo. It is less unforeseen for rodents, which have never been suggested as likely transmitters of the Ebola virus or reported as reservoirs. Ebola virus does not cause any severe disease in rodents as confirmed by laboratory experiments for rodent models such as house mice, *Mus musculus*, guinea pigs, *Cavia porcellus*, and Syrian golden hamsters, *Mesocricetus auratus* (Claire et al., 2017). In our study, we show that there was a differentiated reaction to animals consumed revealed by both, the market surveys and the interview surveys, clearly indicating that those animal groups that have been linked to EVD were still not considered to be safe to eat.

In contrast to the mammal groups, we obtained intriguing patterns for the consumption of reptiles. We observed that the number of reptiles increased significantly during the immediate post-Ebola phase, as mammal trade collapsed. We suggest that this was because reptiles replaced the loss of other wild meat species, in this case mammals. The fact that turtles and tortoises (especially freshwater species) were the most affected by this trade increase is consistent with the fact that (1) chelonians are considered a delicacy by large number of people in West Africa (Luiselli et al., 2019), and (2) by the fact that, despite their heavy population decline (Stanford et al., 2020), they can be still easily captured in large numbers compared to other, more elusive reptiles (e.g., pythons). Indeed, *Kinixys* species are routinely captured, especially in the wet season by snail gatherers since turtles occupy the same microhabitats as *Achatina* snails (Luiselli et al., 2018a), which are heavily consumed and are important in many local dishes. Freshwater turtle (*Pelusios, Pelomedusa* and *Trionyx*) are captured opportunistically in fishnets as bycatch of normal fishing activities or even purposely within

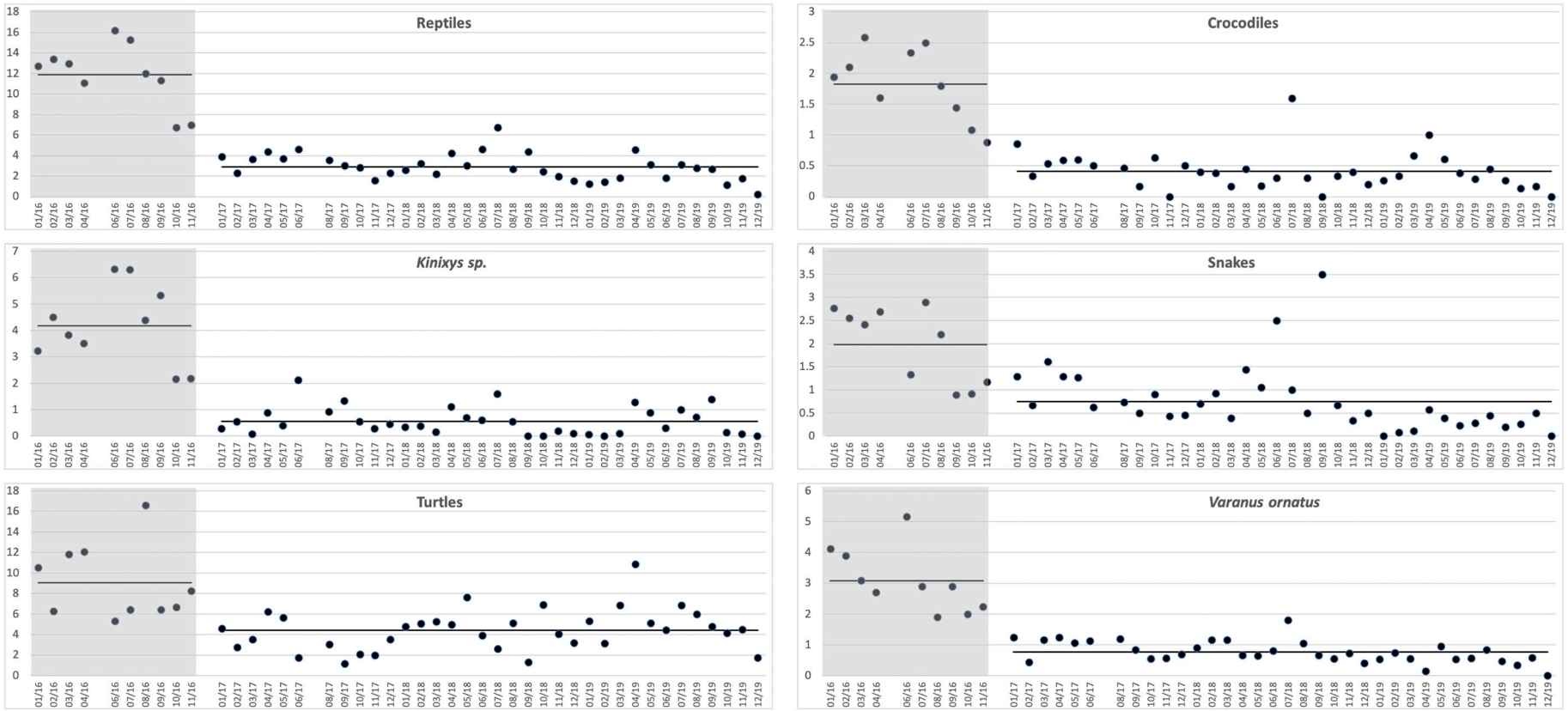

Fig. 3. Trend in the monthly mean number of traded carcasses in nine bushmeat markets in southern Nigeria for monthly surveys between January 2016 and December 2019 for different groups of reptiles. For details see Fig. 2.

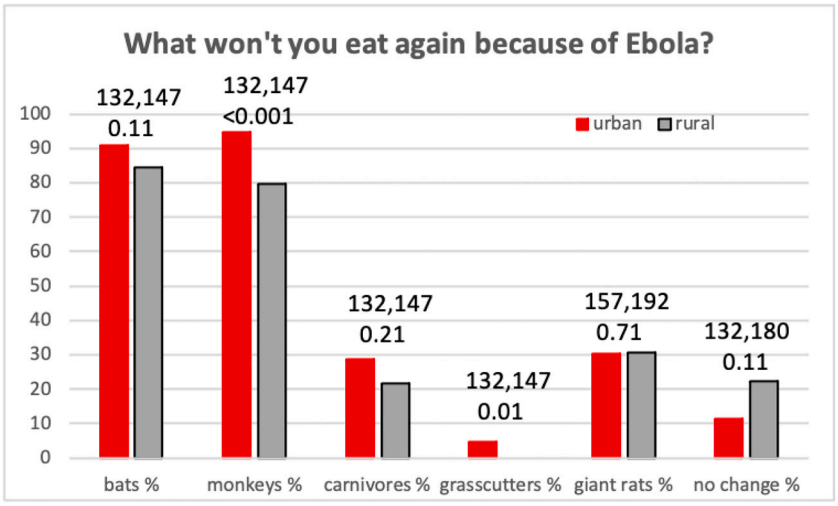

Fig. 4. Answers on the question "Which bushmeat will you not eat again because of ebola?" Shown are percentages of positive answers. Above the graphs for each animal group and for "no change" are shown the sample size for urban respondents, the sample size for rural respondents and the *p*-value resulting from Fisher's exact test for the comparison of replies between urban and rural respondents.

locally-made hoop traps (Luiselli et al., 2020). The collapse of reptiles in general, and chelonians specifically, 2 years post-EVD (when numbers of rodents and antelopes increased) would also indirectly indicate the depletion of reptile numbers, independent of EVD effects, but further affected by increased exploitation by the intensive consumption in the immediate post-EVD phase. Capture-mark-recapture studies in the Niger Delta, including in protected areas, have shown that heavy depletion of forest tortoises (*Kinixys erosa* and *Kinixys homeana*) occurred during the last two decades (Akani et al., 2018; Luiselli et al., 2016), but also of a number of snake species (genus *Python* and *Bitis*) (Reading et al., 2010). There is also indirect evidence for crocodiles, from structured interviews, that populations of these animals are also declining (Eniang et al., 2020). Thus, the impact of EVD in altering wild meat extraction patterns has only exacerbated the already declining trends of the various reptile groups.

How effective the ban was in our study markets is difficult to assess since we were not able to investigate how markets were policed. However, we observed no policing of the wild meat trade during our surveys except during the months in which the virus was affecting the country (July–October 2014), suggesting that enforcement was low after the country was declared free of EVD. Our study quantified the species and numbers on sale in the markets as an indicator of trends in wild meat sales. Therefore, our data may have underestimated what wild meat was available during the ban period, but we are unable to determine by how much. That a significant drop in wild meat occurred in Nigeria can be corroborated by other ancillary data. For example, the monthly sales of dishes of wild meat in restaurants in south-eastern Nigeria fell sharply during the outbreak period and after (Onyekuru et al., 2020). This measure may have been a more accurate indicator of volume of wild meat available than market sales, since in the latter it is possible that some meat may have been sold clandestinely. Even if some trade was driven underground or out of the markets, our data are likely to be a good reflection of reality.

The questionnaires revealed strong location-specific (rural versus urban) and age-specific differences regarding wild meat consumption and attitudes. The large majority of people was worried about Ebola and more than half the interviewee agreed the wild meat poses a transmission risk, indicating that the local education and awareness-raising campaigns were successful. With exception of urban males, the over-60-year old were least informed about the Ebola risk of wild meat, indicating that any future behavioural change will be in the younger age classes. The effects of the theoretical knowledge about Ebola transmission risks on attitudes towards wild meat and actual avoidance of wild meat was most pronounced in the younger two age classes. Although about 10% of the rural or urban under-25-year-old adults and about 20% of the 26-to-45-year-old adults liked wild meat, the under-25-year-old adults abandoned wild meat completely and hardly anybody in the 26-to-45-year age class ate wild meat (Fig. 5). In our study, we show that in the older group (46-to-60-year age class) more than half of rural interviewees ate wild meat whereas 20% of urban respondents consumed it. This difference between young and older classes in wild meat consumption has been demonstrated for other parts of West Africa, independent of Ebola, in urban centres (Luiselli et al., 2018b), and also but to a lesser extent also in rural communities (Luiselli et al., 2019). The main reason for this decline of interest of eating wild meat, especially in the urban areas, is linked to the progressive westernization of young people's habits, with most now thinking that consuming wild meat (outside very special occasions like weddings for instance) is socially unacceptable and perceived as "too primitive" (Luiselli et al., 2018b).

In a previous study on wild meat consumption in a number of southern Nigerian states, including the Niger Delta region, Luiselli et al. (2017) showed that schooling level was significantly negatively correlated with age; with highest schooling typical of younger people ($\leq$25 years) and lowest in older persons ($\geq$51 years). Although we did not record schooling level for interviewees in our study, younger participants in our study consumed wild meat less often. Whether education or age influenced wild meat consumption needs assessing further. Any campaigns to reduce consumption of wild animals needs to be more nuanced, where the emphasis is on the older groups, particularly in urban areas where wild meat is not a necessity but a luxury item (Fa et al., 2003). But, in Nigeria, dependence on wild meat in rural areas is likely to be less important so focussing on reducing wild meat consumption in these localities will not compromise food security of rural inhabitants since other alternative sources of protein are available. Education and awareness-building campaigns are likely to reinforce the avoidance of wild meat by the younger cohorts but help the older generations move away from wild meat. The eventual reduction of wild meat use in areas like those in our study would protect the biodiversity of the region without impinging on the wellbeing of its inhabitants (Fa et al., 2003). However, further studies that clearly establish the dependence of rural peoples on forest foods, in particular, can more clearly determine ways of sustainably harvesting wild meat.

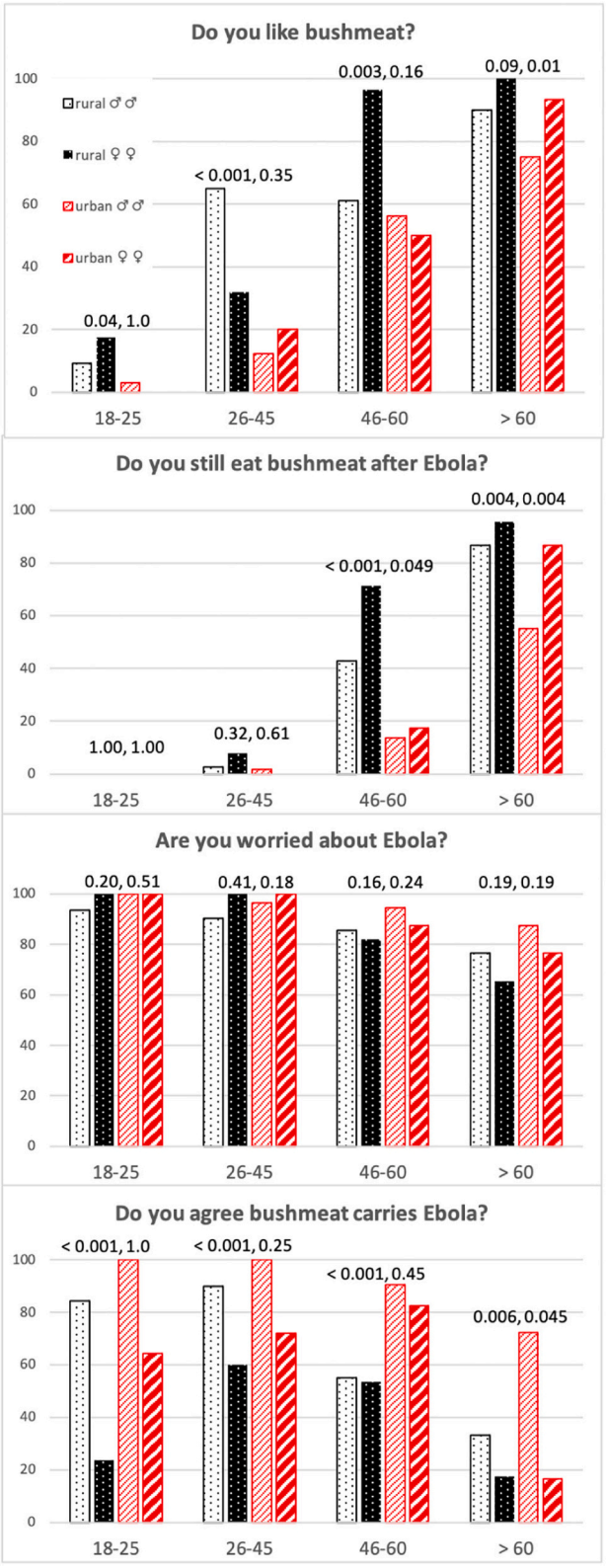

Fig. 5. Answers to various questions regarding attitudes to bushmeat after Ebola. Shown are the percentages answering "yes" for four age classes (18–25 years, 26–45 years, 46–60 years and >60 years old) differentiated according place of living (rural versus urban) and gender. A total of 570 interviews with 326 urban and 244 rural people were conducted. The *p*-values resulting from Fisher's exact test for the comparison between urban and rural respondents (left) and males versus females (right) in for each age class are shown above the graphs.

CRediT authorship contribution statement

Stephan M. Funk: Conceptualization, Data curation, Methodology, Writing- Original draft preparation **Julia E. Fa**: Conceptualization, Writing - Review & Editing **Stephanie N. Ajong:** Investigation **Edem A. Eniang:** Conceptualization, Investigation **Daniele Dendi:** Investigation **Massimiliano Di Vittorio:** Investigation **Fabio Petrozzi**: Investigation **NioKing Amadi:** Investigation **Godfrey C. Akani:** Conceptualization, Investigation **Luca Luiselli:** Conceptualization, Supervision, Project administration, Funding acquisition, Writing - Review & Editing.

Declaration of competing interest

The work is all original research carried out by the authors. All authors agree with the contents of the manuscript and its submission to the journal.

No part of the research has been published in any form elsewhere, unless it is fully acknowledged in the manuscript.

Authors should disclose how the research featured in the manuscript relates to any other manuscript of a similar nature that they have published, in press, submitted or will soon submit to Biological Conservation or elsewhere.

The manuscript is not being considered for publication elsewhere whilst it is being considered for publication in this journal.

Any research in the paper not carried out by the authors is fully acknowledged in the manuscript.

All sources of funding are acknowledged in the manuscript, and authors have declared any direct financial benefits that could result from publication.

All appropriate ethics and other approvals were obtained for the research. Where appropriate, authors should state that their research protocols have been approved by an authorized animal care or ethics committee, and include a reference to the code of practice adopted for the reported experimentation or methodology. The Editor will take account of animal welfare issues and reserves the right not to publish, especially if the research involves protocols that are inconsistent with commonly accepted norms of animal research.

Acknowledgments

This study was funded by the Mohamed bin Zayed Species Conservation Fund, Conservation International, the Turtle Conservation Fund, Andrew Sabin & Family Foundation, T.S.K.J. Nigeria Ltd., IUCN/Species Survival Commission Tortoise and Freshwater Turtle Specialist Group, Aquater S.p.A. and Snamprogetti S.p.A. JEF was funded by USAID as part of the Bushmeat Research Initiative of the CGIAR research program on Forests, Trees and Agroforestry. We are grateful for the constructive comments by two anonymous reviewers.

References

Akani, G.C., Luiselli, L., Angelici, F.M., Politano, E., 1998. Bushmen and herpetofauna: notes on amphibians and reptiles traded in bush-meat markets of local people in the Niger Delta (Port Harcourt, Rivers State, Nigeria). Anthropozoologica 27, 21–26.

Akani, G.C., Dendi, D., Luiselli, L., 2015. Ebola virus effects on the bushmeat trade in West Africa. Afr. J. Ecol. 53, 613–615. https://doi.org/10.1111/aje.12231.

Akani, G.C., Amadi, N., Dendi, D., Luiselli, L., 2018. Do community metrics vary in reptile communities from Niger Delta forests subjected to slash-and-burn agricultural practices? Afr. J. Ecol. 56, 1044–1048. https://doi.org/10.1111/aje.12547.

Alpha, A., Figuié, M., 2016. Impact of the Ebola Virus Disease Outbreak on Market Chains and Trade of Agricultural Products in West Africa. Food and Agriculture Organization of the United Nations, Dakar, Senegal.

Bonwitt, J., Dawson, M., Kandeh, M., Ansumana, R., Sahr, F., Brown, H., Kelly, A.H., 2018. Unintended consequences of the 'bushmeat ban' in West Africa during the 2013–2016 Ebola virus disease epidemic. Soc. Sci. Med. 200, 166–173. https://doi.org/10.1016/j.socscimed.2017.12.028.

Caeiro, F., Mateus, A., 2014. Randtests: Testing Randomness in R, R Package.

Centers for Disease Control and Prevention, 2020. Ebola Virus Disease Distribution Map: Cases of Ebola Virus Disease in Africa since 1976 [WWW Document]. URL. https://www.cdc.gov/vhf/ebola/history/distribution-map.html.

Centres for Disease Control and Prevention CDC, 2016. 2014–2016 Ebola Outbreak in West Africa.
Claire, M.C.S., Ragland, D.R., Bollinger, L., Jahrling, P.B., 2017. Animal models of ebolavirus infection. Comparative Medicine 67, 10.
Dindé, A.O., Mobio, A.J., Konan, A.G., Fokou, G., Yao, K., Esso, E.L.J.C., Fantodji, A., Koussemon, M., Bonfoh, B., 2017. Response to the Ebola-related bushmeat consumption ban in rural Côte d'Ivoire. Agric & Food Secur 6, 28. https://doi.org/10.1186/s40066-017-0105-9.
Duonamou, L., Konate, A., Djossou, S.D., Mensah, G.A., Xu, J., Humle, T., 2020. Consumer perceptions and reported wild and domestic meat and fish consumption behavior during the Ebola epidemic in Guinea, West Africa. PeerJ 8, e9229. https://doi.org/10.7717/peerj.9229 2.
Eniang, E.A., Akani, G.C., Dendi, D., Fa, J., Luiselli, L., 2020. People's perceptions of crocodiles in Nigeria. Herpetol. J. 112–116.
Fa, J.E., Currie, D., Meeuwig, J., 2003. Bushmeat and food security in the Congo Basin: linkages between wildlife and people's future. Envir. Conserv. 30, 71–78. https://doi.org/10.1017/S0376892903000067.
Fa, J.E., Seymour, S., Dupain, J., Amin, R., Albrechtsen, L., Macdonald, D., 2006. Getting to grips with the magnitude of exploitation: bushmeat in the cross–Sanaga rivers region, Nigeria and Cameroon. Biol. Conserv. 129, 497–510. https://doi.org/10.1016/j.biocon.2005.11.031.
Lawson, E.T., Ohemeng, F., Ayivor, J., Leach, M., Waldman, L., Ntiamoa-Baidu, Y., 2017. Understanding framings and perceptions of spillover: preventing future outbreaks of bat-borne zoonoses. Disaster Prev and Management 26, 396–411. https://doi.org/10.1108/DPM-04-2016-0082.
Leroy, E.M., Epelboin, A., Mondonge, V., Pourrut, X., Gonzalez, J.-P., Muyembe-Tamfum, J.-J., Formenty, P., 2009. Human Ebola outbreak resulting from direct exposure to fruit bats in Luebo, Democratic Republic of Congo, 2007. Vector-Borne and Zoonotic Diseases 9, 723–728. https://doi.org/10.1089/vbz.2008.0167.
Luiselli, L., Petrozzi, F., Akani, G.C., 2013. Long-term comparison reveals trends in turtle trade in bushmeat markets of southern Nigeria. Herpetozoa 26, 57–64.
Luiselli, L., Akani, G.C., Petrozzi, F., Eniang, E.A., 2016. Threatened tortoises (genus Kinixys) are confined to small portions of forest even inside wide protected reserves in the Niger Delta, Nigeria. Afr. J. Ecol. 54, 256–260.
Luiselli, L., Petrozzi, F., Akani, G.C., Di Vittorio, M., Amadi, N., Ebere, N., Dendi, D., Amori, G., Eniang, E.A., 2017. Rehashing Bushmeat–Interview Campaigns Reveal some Controversial Issues about the Bushmeat Trade Dynamics in Nigeria (Revue d'écologie).
Luiselli, L., Dendi, D., Pacini, N., Amadi, N., Akani, G.C., Eniang, E.A., Ségniagbeto, G.H., 2018a. Interviews on the status of west African forest tortoises (genus Kinixys), including preliminary data on the effect of snail gatherers on their trade. Herpetol. J. 28.
Luiselli, L., Hema, E.M., Segniagbeto, G.H., Ouattara, V., Eniang, E.A., Parfait, G., Akani, G.C., Sirima, D., Fakae, B.B., Dendi, D., Fa, J.E., 2018b. Bushmeat consumption in large urban centres in West Africa. Oryx 1–4. https://doi.org/10.1017/S0030605318000893.
Luiselli, L., Hema, E.M., Segniagbeto, G.H., Ouattara, V., Eniang, E.A., Di Vittorio, M., Amadi, N., Parfait, G., Pacini, N., Akani, G.C., Sirima, D., Guenda, W., Fakae, B.B., Dendi, D., Fa, J.E., 2019. Understanding the influence of non-wealth factors in determining bushmeat consumption: results from four west African countries. Acta Oecol. 94, 47–56. https://doi.org/10.1016/j.actao.2017.10.002.
Luiselli, L., Akani, G.C., Ajong, S.N., George, A., Di Vittorio, M., Eniang, E.A., Dendi, D., Hema, E.M., Petrozzi, F., Fa, J.E., 2020. Predicting the structure of turtle assemblages along a megatransect in West Africa. Biol. J. Linn. Soc. 130, 296–309.
Malvy, D., McElroy, A.K., de Clerck, H., Günther, S., van Griensven, J., 2019. Ebola virus disease. Lancet 393, 936–948. https://doi.org/10.1016/S0140-6736(18)33132-5.
Mann, E., Streng, S., Bergeron, J., Kircher, A., 2015. A review of the role of food and the food system in the transmission and spread of ebolavirus. PLoS Negl. Trop. Dis. 9, e0004160 https://doi.org/10.1371/journal.pntd.0004160.
Mateus, A., Caeiro, F., 2015. The Difference-Sign Randomness Test: A Review. Presented at the International Conference of Computational Methods in Sciences and Engineering 2015 (ICCMSE 2015), Athens, Greece, p. 030002. https://doi.org/10.1063/1.4938768.
Ogoanah, S.O., Oboh, I.P., 2017. Effect of Ebola virus on bush meat sales in Benin City, Edo state, Nigeria. African Scientist 18, 6.
Onyekuru, A.N., Ezea, C.P., Ihemezie, E.J., 2018. Assessment of the structural effects of Ebola disease outbreak on bush meat Enterprise in Nigeria: implications on biodiversity conservation. JAERI 15, 1–13. https://doi.org/10.9734/JAERI/2018/44018.
Onyekuru, N.A., Ume, C.O., Ezea, C.P., Chukwuma Ume, N.N., 2020. Effects of Ebola virus disease outbreak on bush meat Enterprise and environmental health risk behavior among households in south-East Nigeria. J Primary Prevent 41, 603–618. https://doi.org/10.1007/s10935-020-00619-8.
Ordaz-Németh, I., Arandjelovic, M., Boesch, L., Gatiso, T., Grimes, T., Kuehl, H.S., et al., 2017. The socio-economic drivers of bushmeat consumption during the West African Ebola crisis. PLoS Negl Trop Dis 11 (3), e0005450. https://doi.org/10.1371/journal.pntd.0005450.
Oyediran, W.O., M, O.A., O, E.A., A, O.O., T, D.T., 2015. Effects of Ebola (EVD) outbreak on bush meat marketing and consumption in ibarapa central local government area of Oyo State, Nigeria. Current Research in Agricultural Sciences 2, 90–99. https://doi.org/10.18488/journal.68/2015.2.3/68.3.90.99.
Ozioko, K.U., Okoye, C.I., Obiezue, R.N., Agbu, R.A., 2018. Knowledge, attitudes, and behavioural risk factors regarding zoonotic infections among bushmeat hunters and traders in Nsukka, southeast Nigeria. Epidemiol Health 40, e2018025. https://doi.org/10.4178/epih.e2018025.
R Foundation for Statistical Computing, 2018. R.
Reading, C.J., Luiselli, L.M., Akani, G.C., Bonnet, X., Amori, G., Ballouard, J.M., Filippi, E., Naulleau, G., Pearson, D., Rugiero, L., 2010. Are snake populations in widespread decline? Biol. Lett. 6, 777–780. https://doi.org/10.1098/rsbl.2010.0373.
Rouquet, P., Froment, J.-M., Bermejo, M., Kilbourn, A., Karesh, W., Reed, P., Kumulungui, B., Yaba, P., Délicat, A., Rollin, P.E., Leroy, E.M., 2005. Wild animal mortality monitoring and human Ebola outbreaks, Gabon and republic of Congo, 2001–2003. Emerg. Infect. Dis. 11, 283–290. https://doi.org/10.3201/eid1102.040533.
Stanford, C.B., Iverson, J.B., Rhodin, A.G.J., Paul van Dijk, P., Mittermeier, R.A., Kuchling, G., Berry, K.H., Bertolero, A., Bjorndal, K.A., Blanck, T.E.G., Buhlmann, K. A., Burke, R.L., Congdon, J.D., Diagne, T., Edwards, T., Eisemberg, C.C., Ennen, J.R., Forero-Medina, G., Frankel, M., Fritz, U., Gallego-García, N., Georges, A., Gibbons, J. W., Gong, S., Goode, E.V., Shi, H.T., Hoang, H., Hofmeyr, M.D., Horne, B.D., Hudson, R., Juvik, J.O., Kiester, R.A., Koval, P., Le, M., Lindeman, P.V., Lovich, J.E., Luiselli, L., McCormack, T.E.M., Meyer, G.A., Páez, V.P., Platt, K., Platt, S.G., Pritchard, P.C.H., Quinn, H.R., Roosenburg, W.M., Seminoff, J.A., Shaffer, H.B., Spencer, R., Van Dyke, J.U., Vogt, R.C., Walde, A.D., 2020. Turtles and tortoises are in trouble. Curr. Biol. 30, R721–R735. https://doi.org/10.1016/j.cub.2020.04.088.
Vaz, R.G., Mkanda, P., Banda, R., Komkech, W., Ekundare-Famiyesin, O.O., Onyibe, R., Abidoye, S., Nsubuga, P., Maleghemi, S., Hannah-Murele, B., Tegegne, S.G., 2016. The role of the polio program infrastructure in response to Ebola virus disease outbreak in Nigeria 2014. J. Infect. Dis. 213, S140–S146. https://doi.org/10.1093/infdis/jiv581.
WHO, 2014. WHO Declares End of Ebola Outbreak in Nigeria. URL. https://www.who.int/mediacentre/news/statements/2014/nigeria-ends-ebola/en/.
WHO, 2016. Ebola Outbreak [WWW Document]. URL. https://www.who.int/csr/disease/ebola/en/.