

Ecology of the bushmeat trade in West and Central Africa

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Abstract: The bushmeat trade in West and Central Africa embraces a broad range of ecological, economic, and conservation issues. To date, most studies have focused on the economic and conservation aspects of the bushmeat trade, with less emphasis on the ecological implications of wildlife extraction. Here, we analysed available literature on the bushmeat trade in 5 countries in West and Central Africa exploring ecological traits such as niche width breadth and trophic position of the species involved, and habitats impacted. We also examine temporal changes over a 40-year period. Our results confirm that mammals dominated the trade in all studied areas and time periods, in terms of (i) number of species, (ii) number of traded individuals, and (iii) overall biomass. Herbivores were the most common trophic animal guild traded. Forest-specialists were the most abundant in the trade, and in riverine habitats reptile biomass almost as important as mammals. Overall, the most traded species and individuals were non-threatened according to the IUCN Red List. Our temporal analyses indicated that more habitat generalist and water-linked species were traded during 1971 - 2000, but forest dependent taxa predominated during the following decade (2001 - 2010). Additionally, the number of individuals of large-bodied herbivores rose relative to small and medium-sized ones, whereas traded biomass over time increased: (a) in the consumption of super-predators; (b) of large-bodied herbivores, but (c) a significant decrease in consumed biomass of medium and small-bodied herbivores. We suggest that the observed trends may suggest an imminent reduction of large-bodied herbivores and, as a cascade effect, also of super-predators in African moist forests.

Key words: Africa; bushmeat trade; herbivores; hunting.

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Introduction

The bushmeat trade (i.e. the exploitation of wild animals for food) is a significant driver of defaunation in tropical forests (Gandiwa *et al.* 2014), especially in West and Central Africa (e.g., Bahuchet 1992; Bowen-Jones *et al.* 2002; Fa *et al.* 2002; Hoffman & Pilgrim 2005; Jardin 1970). Exploitation levels, primarily of forest mammals, in West and Central African sites has been estimated to be high, with an average of 16,000 kg site⁻¹ year⁻¹, from around 70 mammal species (Fa *et al.* 2005). Most harvested species are antelopes, monkeys, and rodents (and other mammals), but also includes amphibians, reptiles, and birds (e.g., Fa *et al.* 2002, 2005).

Forest-living people have few alternative sources of protein and income than bushmeat (Bakarr *et al.* 2002; Mainka & Trivedi 2002; Nasi *et al.* 2008). Thus, hunting of wildlife may be locally intense, and may threaten entire populations or even species (e.g., see Oates 2011 for the case of some West African primates). Nonetheless, the intensity of bushmeat exploitation may fluctuate even locally due to eventual perturbing events: for instance, the spreading of Ebola virus was accomplished by a considerable reduction of bushmeat consumption in West Africa (Akani *et al.* 2015). High bushmeat demand has been recorded for west and central African countries [Liberia (Ajayi 1979), Ivory Coast (Caspary 2001), Ghana (Cowlshaw *et al.* 2007; de Vos 1978), Cameroon (Muchaal & Ngandjui 1999), Gabon (Lahm 1996; Steel 1994)] and for the Congo Basin as a whole (e.g., Draulans & Van Krunkelsven 2002; Vanwijnsberghe 1996; Wilkie & Carpenter 1999; Wilkie *et al.* 2005). In recent years, bushmeat has shifted from being primarily a protein source for peoples in the region to a more lucrative trade for many suppliers (de Merode & Cowlshaw. 2006; Martin *et al.* 2012; Obioha *et al.* 2012; Wright & Priston 2010). In the whole of West and Central Africa, the bushmeat trade still represents a profitable business (Hart & Hart 1986; Nyaki *et al.* 2014; Wilkie *et al.* 1992; Wilkie *et al.* 2005), even becoming for many villages the only way of direct and indirect maintenance (e.g., Odzala National Park, Republic of Congo; Vanwijnsberghe 1996). In addition, in several areas where agriculture is the first source of income, bushmeat has become the second (Muchaal & Ngandjui 1999). One of the reasons for the bushmeat becoming a profitable business is that, in rural areas of West and Central Africa, wildlife meat is very cheap and

easily available (Wikie *et al.* 2005), while in urban markets it is usually sold at much higher price, and eaten for traditional and cultural reasons and not only for nutritional motivations (Bowen-Jones *et al.* 2002; Wilkie & Carpenter 1999). Thus, the economics of bushmeat entail a commodity chain that is composed, in most of the cases, of hunters/farmer hunters, wholesalers, market sellers, and owners of local restaurants (de Merode & Cowlshaw 2006; Edderai & Dame 2006; Mendelson *et al.* 2003). In West and Central Africa, the bushmeat trade has generated significant income for all the people involved in the supply chain (Davies 2002; Wilkie & Carpenter 1999), with its economic value equaling 1 % - 1.5 % of the GDP of these countries (Caspary 2001; Davies 2002).

Most of the recent literature for West and Central Africa has treated the bushmeat trade as a conservation issue (e.g., Bakarr *et al.* 2002; Eniang *et al.* 2008; Mainka & Trivedi 2002; Tee *et al.* 2012) of considerable economic impacts (e.g. FAO 1985; Nasi *et al.* 2011), but there has been little discussion on the impact of recorded extraction levels on the ecology of supplying habitats (Nasi *et al.* 2011). For instance, it has remained almost entirely unexplored whether the type of traded species and their ecological role within the ecosystem have changed over time and throughout their geographic range. Instead, the changes of the bushmeat trade dynamics over the years and their implications for both economy and conservation have been more intensely explored. For instance, the changes of the hunting types for bushmeat harvesting throughout Afro-tropical forests were studied intensely (from snares to shot-gun, see Fa *et al.* 2005; Kümpel 2006; Lahm 1993; Oates 1996; Van Vliet & Nasi 2008; Wilkie *et al.* 1992).

Given this paucity of information on the ecology of the bushmeat trade our overall aim was to quantify the type, size, ecological role of the consumed species, inter-habitat differences, and changes in representation of traded species over time. Furthermore, we sought to evaluate the bushmeat data in relation to the current perception of the conservation status of the single species using their IUCN redlist status. We addressed this aim by compiling all available datasets on the bushmeat trade.

Materials and methods

Data sources

To address our main research aim we developed a database from published paper in

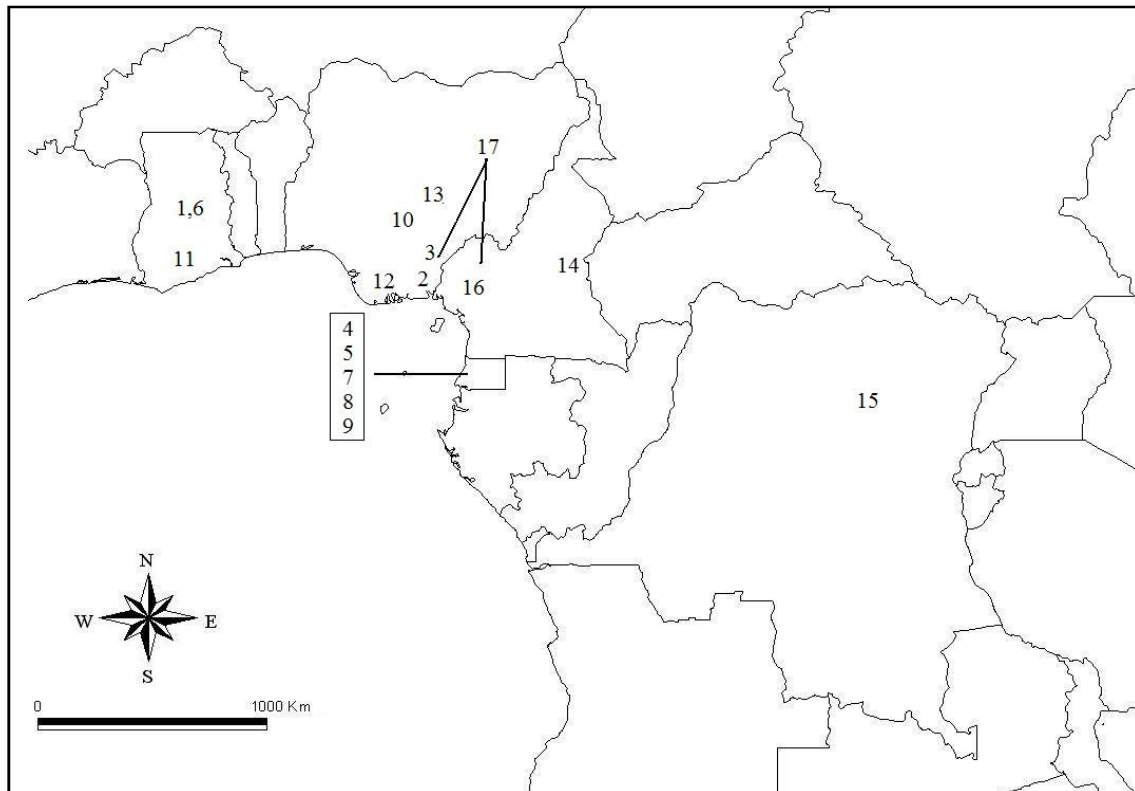


Fig. 1. Map of Western and Central Africa showing the localities from which data were extracted. References: 1 = Crookes *et al.* 2005, 2 = Eniang *et al.* 2006, 3 = Eniang *et al.* 2008, 4 = Fa & García Yuste 2001, 5 = Fa *et al.* 2000, 6 = Falconer 1992, 7 = Gill 2010, 8 = Kumpel *et al.* 2007, 9 = Kumpel 2006, 10 = Martin *et al.* 1983, 11 = Ntiamoa-Baidu 1987, 12 = Okiwelu *et al.* 2010, 13 = Tee *et al.* 2012, 14 = Tieguhong & Zwolinski 2009, 15 = van Vliet *et al.* 2012, 16 = Willcox & Nambu 2007, 17 = Fa *et al.* 2006.

peer-reviewed journals, university dissertations and other technical papers publicly available on the internet (see below). We omitted studies that did not present quantitative datasets ($n = 26$) or contain raw data ($n = 3$). We also excluded studies based on roadside markets (because these often are only temporary; see Olayemi *et al.* 2011), or those that did not contain any explicit reference to the habitat of the study area ($n = 3$). Only those papers that reported actual numbers of (i) animals harvested by hunters and/or (ii) animal present in bushmeat markets were used for the present study.

Data were available for five countries in West and Central Africa (Ghana, Nigeria, Cameroon, Equatorial Guinea, and Democratic Republic of Congo) where the bushmeat trade is known to be especially prominent. Data spanned over approximately 40 years, across a total of 20 different study sites. Considering the broad spatiotemporal elements of the dataset, we assumed that methodological biases, such as the “un-visibility” rate of

the bushmeat economy in each locality (Nasi *et al.* 2008), was evenly distributed across studies and thus not affecting the trends.

In this study, we analysed a total of 404 species \times site records, from 17 bibliographic sources (see Fig. 1; Crookes *et al.* 2005; Eniang *et al.* 2006, 2008; Fa & García Yuste 2001; Fa *et al.* 2000; Falconer 1992; Gill 2010; Kumpel 2006; Kumpel *et al.* 2007; Martin *et al.* 1983; Ntiamoa-Baidu 1987; Okiwelu *et al.* 2010; Tee *et al.* 2012; Tieguhong & Zwolinski 2009; van Vliet *et al.* 2012; Willcox & Nambu 2007; an appendix summarizing the used data is available on request from the authors).

We excluded from the analyses those taxonomic entries with uncertain definitions (e.g., ‘squirrels’), but considered those species that were wrongly identified in the original source yet certainly correctable, such as the alligator (*Alligator mississippiensis*), reported in markets by from Makurdi, Nigeria (Tee *et al.* 2012). This North American species does not occur in West Africa,

Table 1. Summary of the number of markets from which data were acquired in relation to yearly period (10 years timespan) and geographic areas for the bushmeat trade analyzed in the present study. Another additional study, relative to Ghana, was conducted between 1987 and 2002 (Crookes et al, 2005)*, and hence is not included in this table. The number of sites surveyed and the relative habitat types of the various studies are reported in parenthesis. The habitat types of each surveyed site are reported within a specific parenthesis. Thus, for two distinct sites in a same geographic area and in a same study period (for instance, Bioko in 1991-2000), the symbology is: Bioko (2) ('x', 'y') ('x', 'z'), where 'x', 'y' and 'z' are three distinct habitat types as desumed from the original literature sources. Abbreviations for habitat types: (a) primary and mature forest; (b) forest-savannah mosaic; (c) mixed habitats - heterogeneous landscapes; (d) secondary dry forest; (e) secondary moist lowland forest; (f) open and riverine landscapes; (g) wetlands. *habitat types for Crookes et al. (2005): (b, c). **we did not consider data by Fa *et al.* (2006) for this table because it was not possible to assign the precise distribution of the markets in the different habitat types based on the information presented in the original source.

Years	Number of sites surveyed	Geographic area (number of sites surveyed in each country) (habitat types)		
1971 - 1980	1	Nigeria (b, c, d)		
1981 -1990	2	Ghana (c) (b, c)		
1991 - 2000	4	Bioko (2) (a) (a)	Eq. Guinea (a)	Cameroon (e)
2001 - 2010	12	Eq. Guinea (3) (a) (a) (a)	Cameroon (2) (e) (a)	Congo (2) (b, c, e) (b, c, e) Nigeria (5) (a, e) (a, e) (e, f, g) (c) (a)

but there is a relatively similar species, the dwarf crocodile (*Osteolaemus tetraspis*), which is indeed called 'alligator' in Pidgin English by native populations. In this case, we therefore considered the 'alligator' records as belonging to *Osteolaemus tetraspis*. Moreover, because some of the bibliographic sources were outdated, we updated the scientific names of species using the IUCN 2012 Red List. (<http://www.iucnredlist.org>).

Data groupings and categorization

We created a database that included all records of species and number of animals harvested along with the following information: (i) country of origin, (ii) year(s) in which the original data were collected; (iii) number of months in which the original data were collected; (iv) precise geographic location; and (v) local habitat type. Our database showed considerable scatter in years (Table 1) and field effort. Given this scatter, we normalised the data in each study to a yearly unit (i.e. a field effort of 5 months was approximated to 0.5 years and field effort of 5 weeks to 0.1 years).

Habitat types

Habitat types in the various study sites (n = 20 in total, see Table 1), even when they were clearly similar (i.e. in the same regions), were often descri-

bed differently in the original sources. Hence, to standardise the description of habitat types for all species, we condensed the original 105 described habitats to seven main types: (1) primary and mature forest; (2) forest-savannah mosaic; (3) mixed habitats-heterogeneous landscapes; (4) secondary dry forest; (5) secondary moist lowland forest; (6) open riverine landscapes; and, (7) wetlands. Primary and mature forest was overrepresented in the samples (n = 10 out of 20 localities in total), followed by secondary moist lowland forests (n = 7) and mixed habitats (n = 6). Other habitat types were underrepresented (Table 1).

IUCN Red List status

IUCN status of each species was assigned according to IUCN 2012 Red List. We estimated the mean species' body mass from literature sources, using Kingdon (1997) for mammals, Chippaux (2007) and Trape *et al.* (2012) for reptiles, and Ryan & Sinclair (2003) for birds.

Ecological niche breadth

Species' distribution ranges were obtained from the IUCN (2012) Red List, when possible, or from the above mentioned field guides. We classified each species' main habitat (i.e. ecological niche breadth) within its distribution range from White's

(1983) vegetation map of Africa. We defined three distinct groups: (1) restricted forest species (ecological specialists) found in lowland and montane habitats; (2) widespread (ecological generalists) species inhabiting the forest-savannah mosaic, open habitats, and forests, but also occurring in plantations, agricultural lands and human-dominated habitats; (3) species dependant on aquatic habitats (ecologically specialized semi-aquatic species), independently on their distribution. Fish were excluded from our analyses. The attribution of a species to an ecological niche breadth group was also confirmed from observations and field experience of the co-authors, and supported by literature sources (e.g., Chippaux 2007; Kingdon 1997; Ryan & Sinclair 2003; Trape *et al.* 2012). For instance, in the case of the elephant, we attributed the records of *Loxodonta africana africana* to the group 2), and those of *L. a. cyclotis* to the group 1) (Kingdon 1997).

Body size

Body size of all hunted species were grouped into eight classes based on the total sample logarithmic distribution of body masses as follows: (1) > 1 kg; (2) 1 - 5 kg; (3) 5 - 10 kg; (4) 10 - 50 kg; (5) 50 - 100 kg; (6) 100 - 500 kg; (7) 500 - 1000 kg; and, (8) > 1000 kg.

Trophic roles

To analyse the ecological role of each species, we considered four distinct groups: (1) super-predators (Nile crocodile [*Crocodylus niloticus*], African python [*Python sebae*], Crowned eagle [*Stephanoetus coronatus*], Leopard [*Panthera pardus*], Spotted hyaena [*Crocuta crocuta*]), (2) predators (all other carnivorous species), (3) large-sized herbivores (i.e. those species exceeding 15 kg), and (4) medium and small-sized herbivores (i.e. those species with < 15 kg body mass).

Statistical analyses

To assess statistical differences among vertebrate Classes in terms of (1) number of traded species, (2) number of traded individuals, and (3) their relative biomass contributions, we used a chi-square test. Trend and variance analyses were performed using general linear models. General linear models were run using either specimens or biomass/year as dependent variables and year as a continuous predictor. Alpha was set at 5 %. Because there were considerable temporal and

geographic mismatches across the data (Table 1) as the number of studies increased dramatically from 1971 - 1980 (only one site in Nigeria studied) and 1981 - 1999 (2 - 4 site in three different countries) to 2001 - 2010 (12 sites in five different countries), direct comparisons may be biased even if we normalized the data. Thus, analyses of the normalized data set were performed separately for the two time periods: 1971 - 2000 and 2001 - 2010. The IUCN status, and habitat group category, and local habitat type for each species were entered as grouping variables in the general linear models.

Results

Taxonomic representation

A total of 129 vertebrate species were recorded in the literature review. There were significant differences in the number of species appearing by class ($\chi^2 = 155.5$, $df = 3$, $P < 0.0001$), with the number of mammals ($n = 91$) dominating, followed by reptiles ($n = 19$), birds ($n = 14$), and amphibians ($n = 2$). Mammals also dominated the trade in terms of individual animals sold (314, 499), followed by birds (2, 147), reptiles (10, 159) and amphibians (14; χ^2 test, $df = 3$, $P < 0.0001$). The same pattern also emerged as for the biomass contributed by each vertebrate class (χ^2 test, $df = 3$, $P < 0.0001$; data not shown).

Ecological niche breadth of the traded taxa

Habitat specialists dominated the overall sample (96 taxa, 76.1 % of all traded species) as represented by a total of 255, 043 animals traded (78 % of all individuals, 63.2 % of biomass). Amongst the 78 % of individuals traded, the main taxa were *Cephalophus* duikers (32.5 % of total traded individuals and 18.6 % of biomass), rodents (especially Emin's giant pouched rat [*Cricetomys emini*], 7.8 % of the individual traded, 1 % biomass), primates (6.2 % of the traded individuals and 3.6 % of the biomass) and antelopes (37.5 % of individuals, 42 % of biomass). *Cephalophus monticola* provided the largest number of animals in the trade (20.7 % of total individuals), and *Tragelaphus eurycerus* provided the largest biomass volume for a species (20.2 % of biomass).

Habitat generalist species were comprised of 16 taxa, contributing a total of 64,467 animals. Amongst the habitat generalist the grasscutter (*Thryonomys swinderianus*) accounted for the most heavily traded species in terms of number of

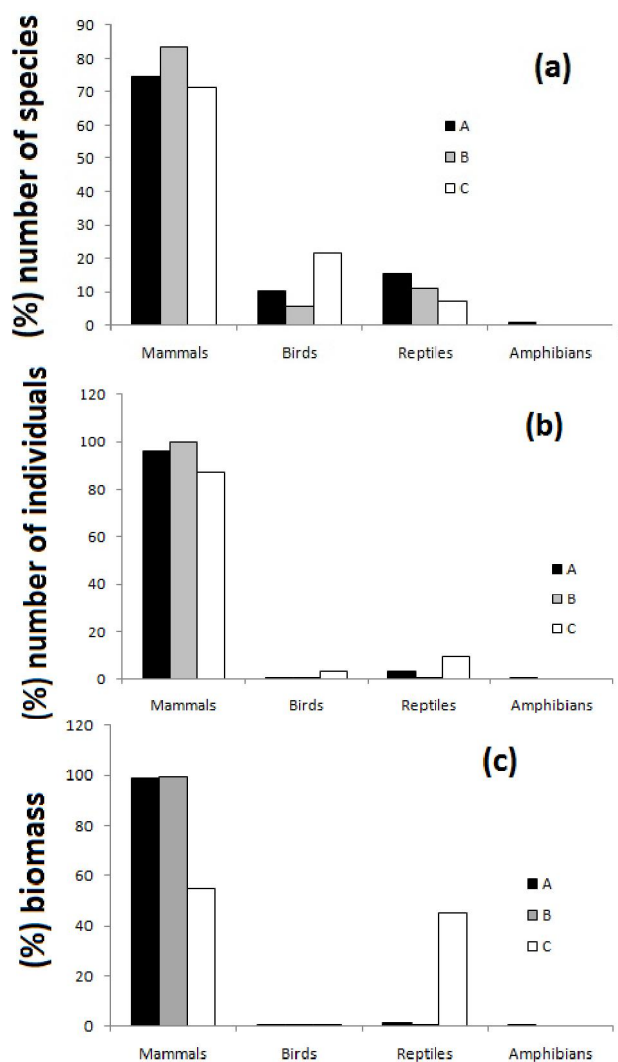


Fig. 2. Percent frequency distribution across habitat groups (A, B or C) of bushmeat individuals and their relative biomass by taxonomic category (class). Graphic (a): number of species; (b): number of individuals; (c): biomass.

individuals (61.4 %), whereas the bushbuck (*Tragelaphus scriptus*) accounted for the greatest biomass (24.5 % biomass).

Aquatic habitat specialists included 14 species and 7,314 individuals traded, with sitatunga (*Tragelaphus spekii*) dominating in terms of number of traded individuals (accounting for 56 % of the whole trade) and the Nile crocodile (*Crocodylus niloticus*) dominating in terms of biomass (49.9 % of biomass).

By taxonomic group, distribution of traded animals and biomass varied significantly between habitats in all cases (Fig. 2.; $P < 0.0001$, χ^2 test). Mammals dominated in primary/mature forests,

forest-savannahs and mixed habitats, and reptiles in riverine habitat (in all cases, $P < 0.01$, χ^2 test).

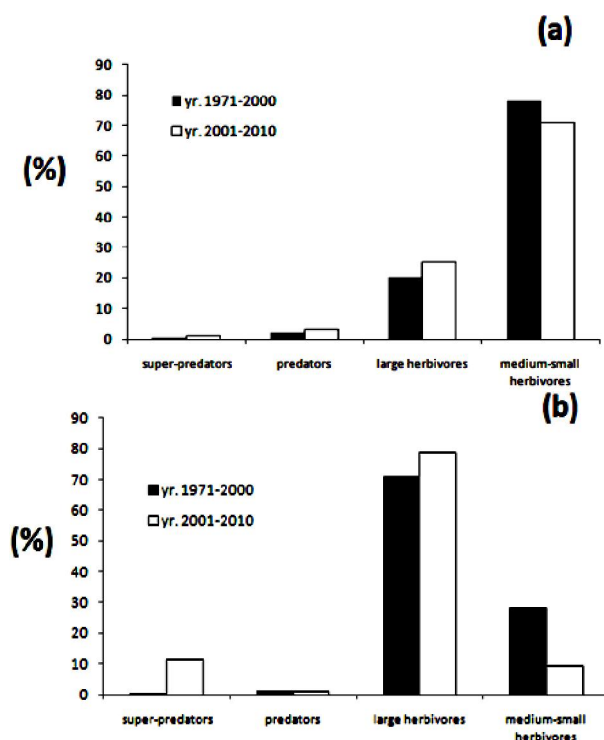


Fig. 3. Percent contribution of the various ecological trophic levels to the bushmeat trade in the two time subsamples; (a) in terms of number of traded individuals; (b) in terms of traded biomass. See text for the statistical tests.

Temporal patterns

Over time the composition of animals traded changed significantly according to their trophic position (Fig. 3a, b). Specifically, while there was no change over time in terms of numbers of traded individuals according to their trophic position ($\chi^2 = 3.61$, $df = 3$, Monte Carlo $P = 0.284$; Fig. 3a), there was a statistical change in terms of biomass ($\chi^2 = 21.95$, $df = 3$, Monte Carlo $P < 0.001$), with a significant increase in trade of super-predators and of large-sized herbivores, and a significant decrease in the consumed biomass of medium and small-sized herbivores (Fig. 3b).

IUCN categories

The great majority of the species in the trade were non-threatened according to IUCN red list, with only 5.6 % of species being in the higher threatened categories (Fig. 4). Amongst the highly threatened species, the total number of specimens

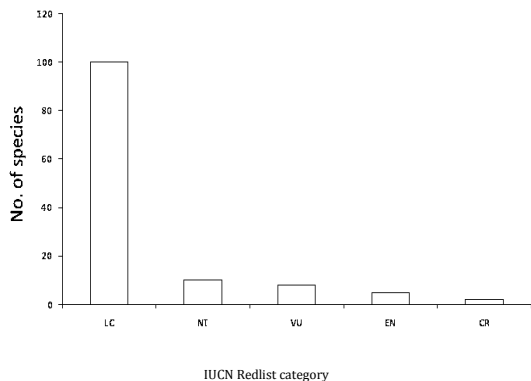


Fig. 4. Distribution of the species observed in the bushmeat trade in relation to IUCN categories (data from IUCN 2012). Symbols: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Lower Risk/Near Threatened; LC = Least Concern.

of CR species was low ($n = 1,193$, 0.36 % of the total traded), and the same was true for the number of individuals of EN species ($n = 5,146$; 1.57 %). Specific quantitative figures revealed that, within the CR and EN categories, the two most frequently traded species were the primates *Mandrillus leucophaeus* ($n = 4,195$ recorded specimens) and *Ptilocolobus pennanti* (1,112 specimens). Other threatened primates sold in bushmeat markets included western lowland gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*), Preuss's guenon (*Cercopithecus preussi*), and bonobos (*Pan paniscus*).

General linear models

From 1971 to 2000 there were no trends in the specimens/year extraction rate among habitats, but a reduction trend in the CR ($r = -0.447$, $P < 0.05$) and EN species ($r = -0.513$, $P < 0.001$). Similarly, there were no trends in biomass from 1971-2000 (in all cases, $r < 0.10$, $P > 0.45$). For the period 2001-2012 (Fig. 5), there was an increase in extraction trend in moist forests ($r = 0.422$, $P < 0.05$), open landscapes ($r = 0.612$, $P < 0.005$), forest-savannah mosaic ($r = 0.387$, $P < 0.05$), and (ii) an increasing extraction trend was detected for the LC species ($r = 0.336$, $P < 0.05$). In terms of biomass there was no significant trend in forest savannah mosaic explained by the higher extraction of lower body mass species at the end of the considered period. However, there was a significantly increasing extraction on LC species ($r =$

0.683, $P < 0.01$), and a highly significant increasing trend in biomass extraction in VU species associated to forest ($r = 0.635$, $P < 0.01$) and moist forest ($r = 0.552$, $P < 0.01$) (Fig. 5) due to the greater body size of the extracted species. In fact, considering the capture trend relative to body mass classes in the second time period there was a significant positive trend in the 1 - 5 and 5 - 10 kg prey categories (Spearman's rank correlation coefficient = 0.438, $P < 0.05$), which was mainly due to an increase of greater body size prey extraction in moist forest habitats, where 0 - 1 kg class decreased.

Discussion

Mammals clearly dominated the bushmeat traded in all the study sites and throughout all time periods, which matches previous studies (e.g., Davies & Brown 2007; Fa *et al.* 2006; Robinson and Bennett 2000, for a review). Some taxonomic groups (reptiles and amphibians) were probably underrepresented in the sample studied because of a higher difficulty in species identification and the distinct focus on mammals in some studies. This lack of herpetofauna can also be indirectly confirmed by the scarce numbers of tortoises and turtles reported in the studies analysed, whereas these reptiles were reported in proportionally much higher numbers in herpetologically-oriented bushmeat market surveys of the Gulf of Guinea region (Akani *et al.* 1998; Luiselli 2003; Luiselli *et al.* 2013). However, it could not be excluded that herpeto-oriented markets were not surveyed in several of the bushmeat surveys: for instance, in the Niger Delta, there are some markets which sale specifically turtles and tortoises and where other categories of bushmeat are scarcely traded (such as in Aven, Patani Local Government Area, Ohimain *et al.* 2014). In these local markets, the amounts of traded reptiles was by far greater than in more generalist markets usually sampled by scientists. Nonetheless, mammals greatly overrepresented the other vertebrates in bushmeat markets, and they can be considered the main preference and target for bushmeat hunting.

Forest-specialist species dominated the trade, both in terms of individuals and relative biomass. This domination by forest-specialists is likely due to the preponderance of forest habitats across the surveyed sites, although more bushmeat activities in forest could not be ruled out. Indeed, previous studies showed that higher harvest levels came from humid forest than savannah ecosystems, and

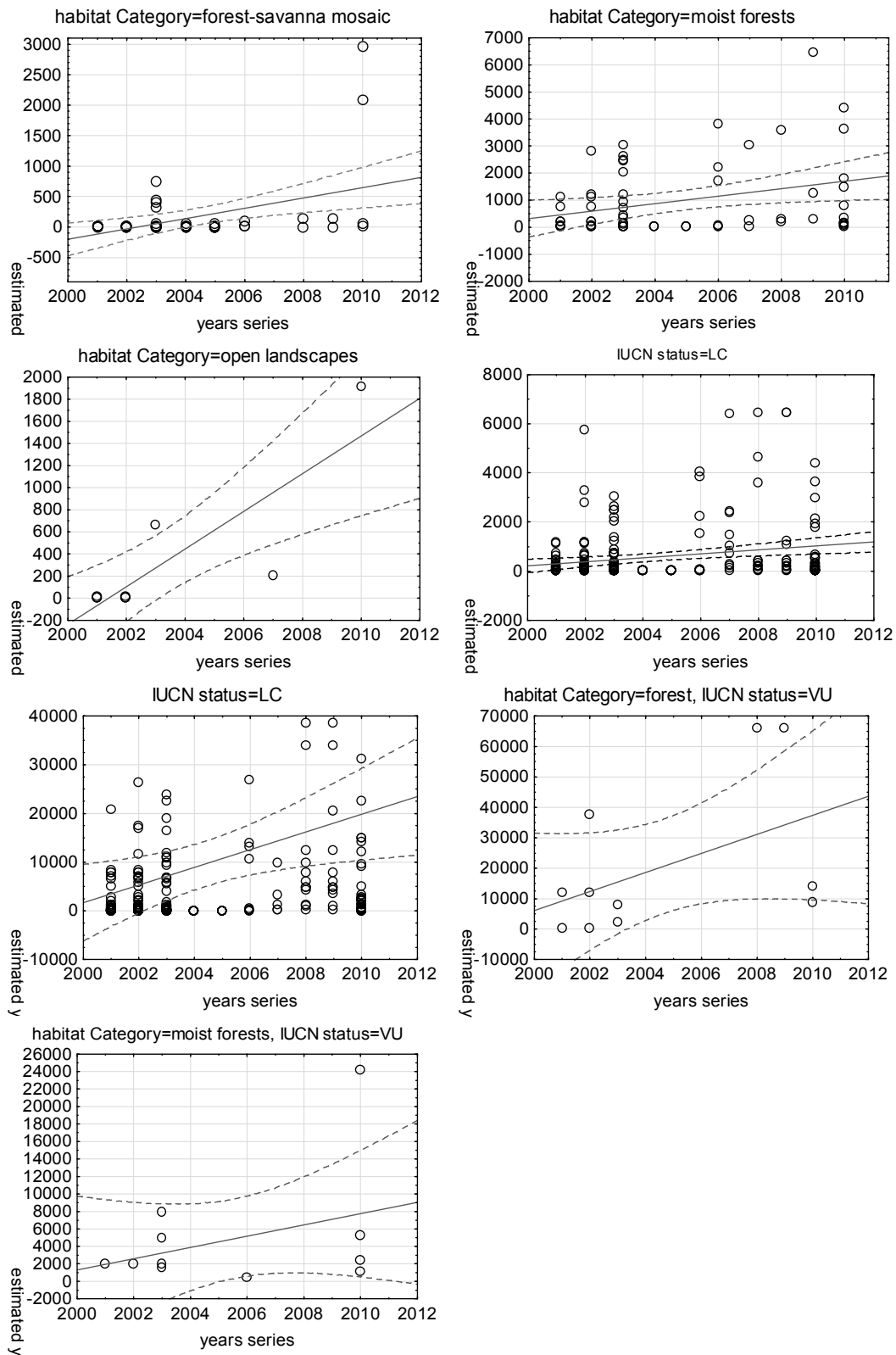


Fig. 5. Scatterplots of the significant relations pointed out by the GLM performed on the second sub-sample and estimated entering either specimens or biomass/year as dependent variable, year series as continuous predictor and IUCN status, and habitat category as as grouping variables. See text for details.

that this evidence may appear to be paradoxical, given the much greater productivity of the latter (Brown & Williams 2003). This apparent paradox may be due to the higher potential of savannah ecosystems to support domesticated fauna, and consequently the associated cultural preference for farmed meat in such areas (Chardonnet *et al.* 1995). However, Fa & Peres (2001) pointed out that other factors may be responsible for the observed patterns, including the abundance and accessibility which certainly influence levels of human dependence (Fa & Peres 2001).

Reptiles were as important as mammals in riverine habitats, at least in terms of traded biomass. The importance of reptiles is due to the contribution given by crocodiles (mainly *Crocodylus niloticus suchus*), which are locally abundant (e.g., Chirio & LeBreton 2007) and in general are quite easy to kill with appropriate shot-guns both during daylight time (when they spend considerable time basking on the river banks) and during night time (when their eyes are clearly reflected using torches; Ross 1998). In addition, the meat of crocodiles is valued and the skin can be traded for leather (Ross 1998).

The great majority of the species (and of the number of individuals) involved in the trade was neither threatened according to IUCN criteria nor showed any shift in pattern over time. Nonetheless, this pattern does not deviate from the expected distribution of threatened categories for the vertebrate species of the study region. Indeed, in the five countries analyzed for this review, both mammals (Schipper *et al.* 2008) and reptiles (Böhm *et al.* 2013) showed a consistent pattern of high species richness but low proportion of threatened taxa. This evidence suggests that bushmeat hunting activities are not specifically targeted on endangered species, but rather are likely determined more by hunting opportunities. Indeed, previous studies indicate that hunters are opportunistic, based on the local availability of wildlife (e.g., Rentsch 2012). However, even if the traded numbers of individuals of threatened species were low. If they are from populations that are already quite low, then the taking of a few individuals could have a significant ecological effect. Thus, our data do not support the notion that the bushmeat trade is sustainable.

Forest species were traded more intensively during the period 2001 - 2010, whereas habitat-generalists and water-linked species were more intensively traded in 1971 - 2000. This change may

be partly due to a habitat-type sampling bias related to the study sites (see Table 1 to appreciate the distribution differences between the two temporal subsamples in terms of number of sites with forested habitat). Alternatively, the observed pattern may be due to the fact that, in the last decades the growing request of bushmeat has created an emerging novel business role of the professional hunter. Indeed, historically most bushmeat was harvested by farmers as a surfeit for the consumption and the gain (e.g., Ajayi 1979; Davies & Brown 2007). So the species hunted were mainly those living around the agricultural fields (e.g., *Thryonomys swinderianus*). Now, although the surfeit hunter is still very present in most of tropical Africa, professional or semi-professional hunters spend considerable time on bushmeat harvesting, and to maximize their profit they enter deep inside the forests where the animals move less or more abundant (e.g., Davies and Brown 2007).

The greatest part of the hunting pressure was towards herbivores (e.g., ungulates, rodents, primates), with a significantly positive trend over time in the hunting of 1 - 5 and 5 - 10 kg body mass preys, while the 0 - 1 kg class decreased during the second sub-sample. We suggest that the shift in mean body size of harvested animals may depend on the fact that, in the recent years, use of the shotguns increased sharply (van Vliet & Nasi 2008), thus allowing a quick and greater investment return when large bodied mammals are hunted (Oates 1996; Waltert *et al.* 2002). In terms of trophic levels, the increased average size of the harvested species might imply an indirect effect (via a density reduction of large sized prey) on the super predators and large-size predators (i.e. pythons, crocodiles, leopards), which are the natural predators of large-sized herbivores. Such an increase in the size of harvested animals may have considerable implications for altering the ecological dynamics of the environments exploited for the bushmeat trade. We anticipate that the increasing extirpation of medium to large sized herbivores (due to direct hunting) may produce a decline in the density of the medium and large-sized predators (due to increased hunting rate and indirect cascade effects of the reduced food availability), and in the long term this will produce a significant loss of species in this trophic level of the ecosystem. Similar types of relationships between abundances of prey and predators are already well known in the literature, also with

respect to medium- and large-sized mammals. Ultimately increased abundances of carnivores (over-predation pressure; the same as in our study system with heavy human predation being the cause) may cause a decline in the herbivores, which may in turn produce a population collapse in carnivore density (e.g., Ballard *et al.* 2001, for a review).

Another important issue that should be considered when interpreting the results is the possible spatial autocorrelation, given that several studies (i.e. those performed in Bioko Island, Rio Muni, and south-eastern Nigeria and western Cameroon) came from nearby areas, with similarity in habitat types, ecological conditions, presence and possibly also relative abundance of species, and uses and traditions of local people communities. Hence, to better understand the ecological attributes of the bushmeat trade, further research should be done in regions different from the ones already repeatedly surveyed, such as Sierra Leone, Liberia, Togo, Benin, and Central African Republic, from where no quantitative data are available.

Overall, our study confirms that there has been a detectable dynamic in hunting pressure, with shifting pressure (increasing) in different habitats and on prey of different body size, due to a plethora of factors including spreading of weapons, relative availability of game animals, and changing attitudes of hunters (e.g., Akani *et al.* 2016). If our findings are correct, the main effect of the bushmeat trade in the decades to come will be the creation of a living world of small-sized prey and predators within the remnant forests of West and Central Africa, similar to what is happening with fish communities because of overfishing (Allan *et al.* 2005).

Potential biases may have considerably affected the outcome of our analysis. High “un-visibility” rate of the bushmeat economy may compromise objective data collection (Nasi *et al.* 2008), and also the recent changes in the scopes of modern bushmeat research and emerging conservation imperatives may have remarkably influenced the data that are available to review (e.g., see Coad 2007; Karesh *et al.* 2005; Macdonald *et al.* 2012). Because of these biases, it remains partially unclear whether the temporal changes highlighted by the present review are merely due to changes in research focus, or actually due to changing human interaction with bushmeat changes in the bushmeat trade.

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