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CONSUMING WILDLIFE – MANAGING DEMAND FOR PRODUCTS IN THE WILDLIFE TRADE

Research Article

Saving rodents, losing primates—Why we need tailored bushmeat management strategies

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Abstract

1. Efforts to curb the unsustainable wildlife trade in tropical forests conceptualize bushmeat as a generic resource, exploited by a homogeneous group. However, bushmeat is composed of miscellaneous species differing in risks of zoonotic disease transmissions, sensitivity to hunting and abundance. If people choose these species for varying reasons, mitigation approaches that neglect specific drivers would likely target abundant species, e.g. rodents. Meanwhile, rare species of greater conservation relevance, like many primates, would be overlooked. Additionally, if reasons vary between user groups, their responsiveness to interventions may differ too.
2. We assessed this possibility for three common strategies to mitigate bushmeat use, which are: development-based—reducing reliance on bushmeat; educational—increasing environmental and school education; and cultural—promoting environmentally friendly habits.
3. We interviewed 348 hunters, 202 traders and 985 consumers of bushmeat around Taï National Park, Côte d'Ivoire, and tested if factors related to the above strategies affected selection for primates, duikers and rodents.
4. Our analyses revealed that people chose taxa for very different reasons. Users with shared characteristics favoured similar taxa; hunters economically reliant on bushmeat income targeted primates and duikers, while hunters and consumers nutritionally reliant on wildlife protein preferred rodents. Different groups used the same taxa for varying reasons. For example, hunting of primates was associated with economic needs, while their consumption appeared a matter of status. Meanwhile, cultural habits, like religion, specifically affected consumption and

taboos inhibited the use of primates; environmental awareness was linked to lower utilization of most taxa within most user groups.

5. Our results demonstrate that educational-, cultural-, and development-based strategies may address different needs and taxa. Consumers may present a key target group, as they rejected rare species for multiple cultural and educational reasons. Notably, the widespread effect of environmental awareness could facilitate large-scale demand-reduction approaches. Nevertheless, there is no one-size-fits-all solution and campaigns need to be tailored to specific taxa and user groups. Ultimately, clear target definitions, prior in-depth research, community-driven solutions and tools from marketing and psychology may help to design novel strategies that encompass the diversity of bushmeat species and its users.

KEYWORDS

bushmeat crisis, conservation, environmental awareness, hunting, poaching, West Africa, wildlife commodity chain, wildlife trade

1 | INTRODUCTION

Unsustainable hunting of wildlife for human consumption and trade throughout the tropics is increasingly tied to the extinction of wildlife populations and human development challenges. This includes food insecurity, emergent disease risks and zoonotic spillover events, which are linked to outbreaks of Ebola, SARS, MERS and likely of the novel pneumonia COVID-19, which, even in its early stages has caused a significant global health, public and economic crisis (Andersen, Rambaut, Lipkin, Holmes, & Garry, 2020; Hutt, 2020; Nielsen, Meilby, Smith-Hall, Pouliot, & Treue, 2018; Nielsen, Pouliot, Meilby, Smith-Hall, & Angelsen, 2017; Olival et al., 2017). Attempts to curb the harmful effects of this 'bushmeat crisis' often conceptualize bushmeat as a generic resource exploited by a single homogeneous group of users (van Vliet, 2018). However, over 500 bushmeat species have been described in Sub-Saharan Africa (Fa & Brown, 2009), varying greatly in sensitivity to hunting pressure and risk of zoonotic disease transmission (Olival et al., 2017; Petrozzi et al., 2016). For instance, slow-reproducing and consequently more vulnerable species like primates are overhunted in many areas, although they typically represent only a small percentage of the combined bushmeat biomass (Fa & Brown, 2009; Petrozzi et al., 2016). In fact, around 80% of the total bushmeat biomass in West and Central Africa consists of robust and fast-reproducing generalists including porcupine, pouched rat, small-bodied duikers and antelopes (Fa & Brown, 2009; Petrozzi et al., 2016). These species persist in overhunted landscapes and are a crucial component of food security and livelihoods throughout rural areas in Sub-Saharan Africa (Friant et al., 2020; Nasi, Taber, & Van Vliet, 2011; Nielsen et al., 2017, 2018).

Moreover, replacing this food source with alternative animal protein could substantially increase unsustainable exploitation of other resources including fish stocks, and lead to habitat degradation to provide grazing land (Brashares et al., 2004; Nasi et al., 2011). The extent to which primarily rare or abundant species are targeted can vary between hunters (Catarina et al., 2017; Jones, Keane, John, Vickery, & Papworth, 2018) and consumption choices can also have species-specific drivers (East, Kümpel, Milner-Gulland, & Rowcliffe, 2005; Foerster et al., 2012). Thus, if bushmeat is considered as a homogeneous resource, an analysis of the determinants of bushmeat utilization would primarily reflect the drivers of the utilization of abundant species with a high share of the total bushmeat biomass. At the same time, rare species of greater conservation relevance would likely be overlooked. Paradoxically, with drivers varying between species, the probability of a successful outcome from a conservation strategy designed to reduce overall bushmeat utilization, would decline with a given species' rarity. Another often neglected element is the structure of the bushmeat trade chain, which involves multiple actors, intertwined through complex demand–supply dynamics (Bachmann et al., 2019; McNamara et al., 2016). In wildlife depleted areas, hunters may determine the supply (Allebone-Webb et al., 2011; McNamara et al., 2016), whereas in remote areas with higher availability of bushmeat, the few present traders may determine which species reach urban markets by controlling supply to increase profit (Allebone-Webb et al., 2011). In urban centres, with a rich and diverse offering of bushmeat, consumer preferences may determine supply, and thus hunting pressure for specific taxa (Allebone-Webb et al., 2011). If different user groups prefer the same taxa for varying reasons, they would likely respond differently to incentives, which could lead to dissimilar, or in the worst-case, opposing effects (Jones et al., 2018). For instance, economic development would presumably reduce overall hunting pressure where hunting is driven by poverty, as appears common in rural areas (Nielsen et al., 2017). However, the same economic development could increase demand, because increased disposable income permits consumers to purchase more bushmeat, and specifically coveted expensive delicacies (Cowlishaw, Mendelson,

& Rowcliffe, 2005; East et al., 2005). Higher demand for certain species can substantially inflate prices, which can motivate hunters to overexploit populations, leading to local extinction events (Waite, 2007). Consequently, if determinants of preference for the same taxa differ between user groups, regulation strategies must encompass these variations in the trading network.

The most common strategies to reduce bushmeat hunting are (a) development-based, such as reduction of economic and nutritional reliance on bushmeat (van Vliet, 2011); (b) educational, through increasing formal and environmental education (Nasi et al., 2008); or (c) cultural, such as promoting environmentally friendly habits (Mbotiji, 2002). However, it remains unclear whether the paradigm of bushmeat as a homogeneous resource holds, and hence whether these strategies can be applied universally, or affect species and user groups differently. In this paper, we applied a large dataset of interviews along the bushmeat chain, to test whether nutritional and economic reliance on bushmeat, environmental awareness and education level, as well as cultural habits affect selection on the taxon-level differently by different user groups. We chose user groups involved in the production (hunters), the distribution (traders) and the consumption (consumers) of bushmeat. With this detailed insight into taxon-specific drivers at multiple user group levels, we aim first to understand whether there is a general need for specifically tailored interventions, and second, to provide the knowledge for informed development of innovative strategies for sustainable management of the bushmeat sector.

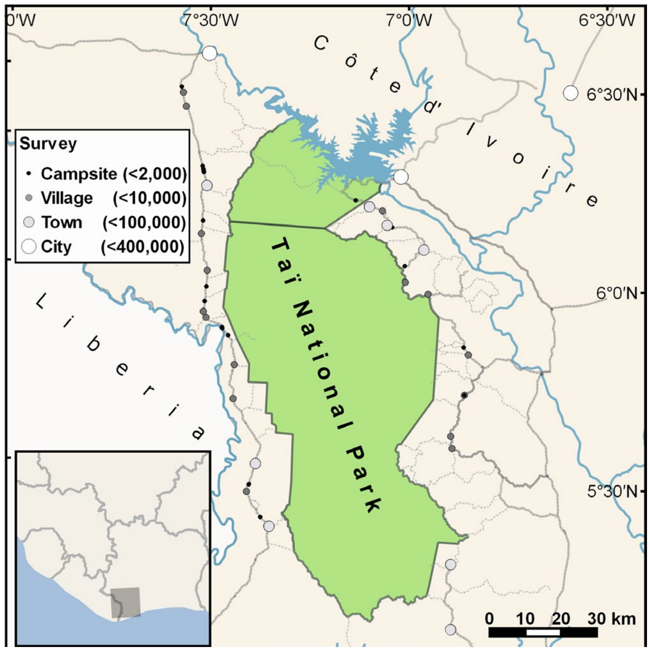

FIGURE 1 Survey: urban and rural locations

2 | METHODS

2.1 | Study site

We conducted the study around Taï National Park (TNP), located in southwest Côte d'Ivoire. Embedded in an agricultural mosaic, the TNP comprises 5,360 km^2 rain forest and is one of the last remaining wildlife habitats in this region. However, the decline of wildlife due to hunting is alarming and has already led to the 'empty forest syndrome' in the eastern parts of the park (N'Goran et al., 2012). The principal sources of income are agricultural activities, and 46.3% of the human population live below the poverty line (ENV, 2015). The cultural landscape is diverse, with 65 ethnic groups. Local ethnic groups comprise approximately 30% of the total population (Bété, Guéré, Krou, and Wobé), and the area also harbours immigrants originating from Burkina Faso and Mali (ENV, 2015).

2.2 | Data collection

We conducted interviews from January to August 2015 in 47 settlements around TNP (Figure 1). We randomly selected settlements within a buffer of 25 km from TNP and interviewed bushmeat vendors in three adjacent urban bushmeat trading points. We used a strategic sampling strategy surveying each *n*th household, depending on settlement size and achieved sampling coverage between 3.3% and 33.3% for settlements smaller than 25,000 inhabitants. For larger settlements, we used a two-stage cluster sampling method, whereby we first randomly selected one-third of the roads and then divided the adjacent houses by the desired sample size, and sampled again each *n*th household (Galway et al., 2012). To provide generalizable results over the mean of all settlements, we stratified our data collection according to settlement size (Appendix 1, Table A.1.1). We approached bushmeat traders through the local meat trading association, in which they were officially organized. Due to the lack of formal organizational structures of hunters, we used a 'snowball' sample method to recruit hunters, whereby former interviewees and informants (hunters) recruited new participants (Patton, 1990). Coincidently, our study was conducted during the West African Ebola crisis. Government authorities increased prohibition measures, closed bushmeat markets and persecuted hunting in order to prevent a spread of Ebola from neighbouring countries to Côte d'Ivoire. Most actors abandoned their bushmeat-related activities, and thus without the usual fear of prosecution (Kouassi, Normand, Inza, & Boesch, 2017), agreed to provide detailed insights, thereby contributing to generating one of the largest available datasets describing a bushmeat commodity chain. As self-report and recall data can be biased (Gavin, Solomon, & Blank, 2009; Golden, Wrangham, & Brashares, 2011; Jones, Andriamarovololona, Hockley, Gibbons, & Milner-Gulland, 2008), we extensively cross-evaluated our dataset and evaluated the likelihood for false-positive results of our analyses (see Section 4).

2.3 | Ethics statement

Permission for this study was requested from all administrative and informal levels (settlement, district, national level, NGOs, park authorities, settlement chiefs and elders) and additional permissions from local residents were obtained via a public settlement meeting. Work was conducted in strong collaboration with local authorities from the various ethnic groups. Ethical guidelines were in accordance with the declaration of Helsinki. The compliance with ethical standards was examined by the Ethics Council of the Max-Planck Society (Application No: 2020_15) and during the application process for a research permit by the Ivorian Government Institutions (research permit 105/MESRS/DGRSIT/mo). Prior to each interview the purpose of the study, the use of the data, anonymity, confidentiality and the voluntary basis of responses were explained and interviews were only conducted after informed consent. All precautions to ensure anonymity were strictly adhered to. We avoided visiting hunters or traders in their homes, to also prevent later problems for informants. We refrained from conducting hunter follows or quantitative surveys of the remaining trade due to the highly questionable ethics of sending the wrong signals regarding conservation goals, and especially infection risks, in addition to the potential illegality of such activity.

2.4 | Questionnaire design

As the bushmeat ban implemented in 1974 (Ministerial order No 003/SEPN/CAB) was strictly enforced during the EVD outbreak and punished with imprisonment, we focused only on the period (6–15 months) before the outbreak of Ebola, about which respondents felt comfortable openly providing information. We asked hunters and traders to describe an average hunting trip or market day, regarding the number hunted, or quantity traded per each species, their prices, sources and destinations. To avoid miscalculations, the respondents determined the units in which all observations were recorded (per market day, hunting trip, hunting season, day, week, month or year). All hunters operated under the same seasonal variations. We recorded all cash income and number and value of assets owned per household and noted all changes since the outbreak of Ebola (for questionnaire designs see Appendix 1.1). Interviews were conducted by local assistants with prior experience in data collection on regional bushmeat markets and restaurants in French or local languages. To minimize potential bias through recollection error and active misleading, resulting in under- or overestimated values (Gavin et al., 2009; Golden et al., 2011; Jones et al., 2008), we compared data collected by direct and indirect questioning and cross-validated our data through comparison with available datasets from this region (Kouassi et al., 2017; Appendix 1.2). Since we found high consistencies and no evidence of intentional underreporting of species with higher protection status (e.g. 7.3% vs. 7%, Kouassi et al., 2017 utilization of primates), we assume that our dataset accurately reflects reality (Appendix 1.2, Table A1.2) and is suitable to answer our research questions. See also Bachmann et al. (2019).

2.5 | Response variables

To understand why people use a greater or smaller diversity of species, we fitted one LMM (Baayen, 2008; Gaussian error structure and identity link function McCullagh & Nelder, 1989) for each user group, that is, hunters, traders and consumers. The response was the diversity of species measured in the total number of different species utilized per person (Table 1). To further understand what drives selectivity, we fitted a GLMM (Baayen, 2008) with Poisson error structure and log-link function for each user group and taxon separately (i.e. three models for three actor groups times three models for three taxon groups equal to nine models in total; Table 1). Here we focused on orders or subfamilies, which are frequently used and have distinctive habitat requirements and life-history strategies and conservation status, namely primates, duikers and rodents (Fa & Brown, 2009; Petrozzi et al., 2016). We hypothesized that selectivity takes place on these higher functional groups because firstly, households and traders could often only name these broad categories, and since meat was purchased smoked, species identification was further hampered. Secondly, hunting on the species level might still occur opportunistically, whereas genus-specific foraging times and hunting grounds reflect a conscious decision on behalf of the hunter. Rodents were caught in fields, duikers were targeted in protected areas (PAs) and adjacent forests, mainly at night and primates were poached under high risk of detection by rangers during the day in PAs (Kablan et al., 2017). For hunters and traders, the response was the average number of animals hunted or sold per unit time (e.g. hunting or trading day) for each taxon. For consumers, we used the daily frequency of consumption of species in each taxon.

2.6 | Predictor variables

2.6.1 | Predictors associated with development-based strategies

Development-based strategies rest upon the hypothesis that bushmeat utilization can be reduced by diminishing the reliance on bushmeat by providing alternative sources of protein and income (Sylvia & Coad, 2019; van Vliet, 2011). Different forms of reliance on bushmeat can thereby affect selection among species and the overall diversity of species used (Friant et al., 2020). Therefore, we used here several indicators. We included the proportion of bushmeat income in total household cash income, as we expected economic reliance to increase with income generated through hunting or trading activities, following Nielsen et al. (2018). For consumers, we included cash income per capita, as we assume that financial constraints increase reliance on cheap bushmeat (Friant et al., 2020). Furthermore, we assumed that fewer alternatives to bushmeat increase nutritional reliance on bushmeat (Friant et al., 2020). We included, therefore for all user groups, first the average physical availability of alternative proteins (USDA, 1996) including domestic meat and fish, measured as availability per day, and second, the economic accessibility (USDA, 1996) measured as an average price per kg for alternative proteins per settlement. Further information on how we derived these settlement-specific measurements can be found in Appendices 1.3 and 1.5. Lastly, the amount of meat required to fulfil household protein and micronutrient requirements can increase reliance on bushmeat and affect selectivity (Friant et al., 2020). We therefore included the number of dependent children per household, as the pressure to

TABLE 1 Overview of research questions, applied models, error structures, response variables and their definitions, and sample sizes with and without missing values

Research question	Model	Response	Definition	Sample size without missing values	Data	Error structure
What influences the general utilization of species?	1a	Total no. of species hunted/year	Species diversity measured in the total number of different reported species hunted, traded and consumed within the last year. For identification, a coloured guide of occurring species was provided	$n = 232$	Interviews with 348 hunters, 202 bushmeat traders and 985 consumers	Gaussian
	1b	Total no. of species traded/year		$n = 155$		
	1c	Total no. of species consumed/year		$n = 923$		
Why certain taxa and species are targeted?	2a	Number of primates hunted/day	Reported animals hunted or sold per average market day or consumption frequencies per day	$n = 223$	Interviews with 348 hunters, 202 bushmeat traders, 985 consumers	Possion
	2b	Number of primates traded/day		$n = 166$		
	2c	Consumption frequency of primate meat/day		$n = 912$		
	3a	Number of duikers hunted/day		$n = 223$		
	3b	Number of duikers traded/day		$n = 161$		
	3c	Consumption frequency of duiker meat/day		$n = 911$		
	4a	Number of rodents hunted/day		$n = 223$		
	4b	Number of rodents traded/day		$n = 161$		
	4c	Consumption frequency of rodent meat/day		$n = 923$		

provide nourishment or money may be higher for households with more mouths to feed (Bachmann et al., 2019; Kouassi et al., 2017; Overview see Table 2, summary statistic Appendix Tables A.1.4–A.1.6).

2.6.2 | Predictors associated with cultural-based strategies

Culture-based strategies assume that some cultural habits, through regulative functions, prohibitions and differing value orientations are 'environmentally friendlier' than others (Gifford, 2012; van Vliet, 2018). We tested this effect using religious affiliation and adherence to traditional taboos as proxies because spiritual/religious affiliations can promote sustainable resource use (Berkes, Colding, & Folke, 2000; Gifford, 2012; van Vliet, 2018). Similar pro-environmental effects have been associated with traditional hunting rules (Berkes et al., 2000). We included the manner of transmission of hunting knowledge as a proxy for traditional hunting rules as we could not distinguish traditional hunting rules from habits related to modern-day 'witchcraft' or the civil war. Moreover, hunting practices were often family secrets. Like elsewhere, traditional hunting knowledge is passed along generational lines from grandfathers and fathers to sons (Berkes et al., 2000). Currently, hunting has moved from wildlife-scarce areas into more wildlife-abundant PAs, which bear the risk of fines or imprisonment. Hence, fathers hesitate to take their sons hunting, which inhibits cultural transmission. We hypothesized that hunters with hunting knowledge transmitted through the family line by fathers or grandfathers, adhere more closely to traditional practices and thus avoid overexploitation by targeting less rare species than hunters who gathered this knowledge by themselves or obtained it via similar aged peers. (Overview see Table 2, summary statistic Appendix Tables A.1.4–A.1.6).

2.6.3 | Predictors associated with educational-based strategies

Educational-based strategies hypothesize that making informed pro-environmental choices depends first on having the respective knowledge, and second that individuals with higher education are in general more concerned about the environment (Gifford, 2012). Thus, we tested whether the effect of formal education, measured in years of school attendance, and the impact of environmental awareness, assessed by asking respondents whether hunting and consumption of bushmeat have harmful effects on the local fauna, may affect resource use choices (Junker et al., 2015; Kouassi et al., 2017; Overview see Table 2, summary statistic Appendix Tables A.1.4–A.1.6).

TABLE 2 Overview of test predictors, their units, operationalization of measurement and in which models they were included

Predictors	Proxy for	Unit	Measurement	Model
Development-related predictors				
Per capita cash-income	Economic reliance	Income/household size in West African CFA (XOF)	Per capita household income = non-agricultural salaries (pensions, donations, commercial enterprises) + agricultural income (livestock husbandry + yield × price − expenses + income from hunting/trading	Model consumers (Models 1c, 2c, 3c, 4c)
Percentage of cash-income gained with bushmeat	Economic reliance	%	Income from hunting or trading/overall cash household income (agricultural + non-agricultural income + income hunting or trading) × 100	Model hunters/traders (models 1a, b, 2a, b, 3a, b, 4a, b)
No. of dependent children	Economic pressure	Children (>15) per household	Financially dependent children/household	All
Economic availability of alternative protein	Nutritional/economic reliance	Price for alternative protein (XOF)/kg	Fitted values of the random effect of *settlement id* derived from an LMM with the response being *price/kg* and the random effects *settlement id*, *household id* and *protein type* (fish, chicken, cattle, goat, sheep)[a]	All
Physical availability of alternative protein	Nutritional reliance	Availability alternative protein (days/year)	Fitted values of the random effect *settlement id* derived from an LMM with the response *availability of protein/week* and the random effects *settlement id*, *household id* and *protein type* (fish, chicken, cattle, goat, sheep)[a]	All
Cultural-related predictors				
Species-specific taboo	Traditional belief systems	Yes/no	If a person considered the respective taxon as a taboo	Models on the taxon level (models 2a, c, 4a, c; when <10 people had taboos for a taxon, the variable was excluded from the model)
Taboo	Traditional belief systems	Number of taboos	Sum of adhered taboos per respondent	All species diversity models (1a, b, c)
Transmission of hunting knowledge	Traditional ecological knowledge	'Family' 'Not family' 'Alone'	'Family' = learned from father, grandfather, uncle, or brother, 'Not family' = learned from other hunters 'Alone' = self-taught hunter	Hunter models (models 1a, 2a, 3a, 4a)
Religion	Religious belief systems	'Muslim' 'Christian' 'Animist'	Religious affiliation of respondent: Animists included both Atheists and Animists (ENV, 2015). Christians included both Protestants and Catholics. Rare religions were excluded	All; in models 1b, 2b, 3b, 4b, the level Muslim was excluded due to the low number of Muslim bushmeat traders (4 of 202)
Educational-related predictors				
Educationlevel	Formal education level	Years of school	Years of school attendance (literate people without school attendance were scored as having completed one school year)	All
Environmental awareness	Environmental education level	'Don't know' 'No' 'Yes'	People were asked whether bushmeat extraction can be harmful to the local fauna. Answers were grouped into the three categories 'Don't know', 'No' and 'Yes'	All

Note: All variables refer to before the outbreak of EVD.
[a]Further information Appendix 1.3.

2.6.4 | Control predictors

To model people's use of wildlife, controlling for the fact that respondents specified the use in different units (e.g. two Maxwell duikers per week, one red colobus per month) we included the time span (day (1), week (7) or year (365), log-transformed) as an offset term (McCullagh & Nelder, 1989) in the model. Furthermore, we included the species as a random effect (e.g. red colobus

Piliocolobus badius). Unidentified species were assigned to the category unidentified duiker or primate (rodent species could always be named; Appendix 2, Table A.2.1). Due to lack of information on the species level, we did not include this random effect for the models investigating consumption of primates and duikers. We further included potentially influential geographic, demographic and contextual predictors not connected to our research question as control variables. These include residence duration, age, sex and settlement size (Luiselli et al., 2019; Morsello et al., 2015). We included price or availability of a species to control for the possibility that utilization is a function of these. We included settlement, ethnicity (except model 2a) and species (model 2a, b, 3a, b, 4a, b, c) as random effects (Table 1; Appendix Table A.1.8). We excluded some potential important predictors for prey or consumption choices due to theoretical considerations (see Appendix 1.6). (overview see Appendix Table A.1.3, summary statistic Appendix Tables A.1.4–A.1.6).

2.7 | Statistical analyses

We square root transformed the predictors ‘Cash Income per head’ and ‘Education level’ for all consumer models (model 1–4c) and log-transformed ‘settlement size’ for all models and ‘Percentage of cash income gained with bushmeat’ for all trader models (model 1–4b; Table 1; Appendix Tables A.1.4–A.1.6; Tables A.2.2–A.2.13) to achieve roughly symmetrical distributions and avoid overly influential cases. We then z-transformed all numeric fixed effects to a mean of zero and a standard deviation of one to achieve easier interpretable coefficients (Schielzeth, 2010). All theoretically identifiable random slope components were included, but due to complexity issues, correlations between random intercepts and random slopes were omitted (Barr, Levy, Scheepers, & Tily, 2013; Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017; Schielzeth & Forstmeier, 2009; for information about which random slopes were included in which model see Appendix Table A.2.4). We evaluated the possibility of multicollinearity by variance inflation factors (VIF; Field, 2005) determined for models lacking random effects. Model stability was assessed by comparing the estimates obtained for the full dataset, with estimates obtained after excluding levels of the random effects one at a time. This revealed no problematic levels of random effects. We checked for normal distributions of random effects ('BLUPs' sensu Baayen, 2008) by visual inspection of histograms, and for normality and homogeneity of residuals (Gaussian error function), by inspecting qqplots of the residuals and scatterplots of the residuals plotted against fitted values (Field, 2005). This revealed no obvious deviation from these assumptions. We used a likelihood ratio test (LRT) to compare the full model with a respective null model, which lacked the test predictors, but kept all control, fixed and random effects (Schielzeth & Forstmeier, 2009). We encountered several issues, such as complete separation, slightly correlated predictors (VIF > 2) and overdispersion. We included in some Poisson mixed-effects models an 'observation-level random effect' to account for overdispersion (Harrison, 2014; Appendix Table A.1.7). After further extensive sensitivity testing and countermeasures, we found that our results were robust. For an overview of model diagnostics, measures and sensitivity tests see Appendix Table A.1.7.

3 | RESULTS

Overall, the reported number of different species utilized was a maximum of nine by consumers, 15 for traders and 20 for hunters. Primates were the most hunted taxon (32.2%; Figure 2a) and 63.6% of the hunters (n = 223) included primates in their prey. Duikers were hunted at the second highest rate (30.3%; Figure 2a), with 76.2% of hunters catching duikers. Rodents were the least hunted taxa (23.4%) and 70.8% of the hunters harvested rodents. In contrast, the most traded taxa were rodents (46.6%; Figure 2a)

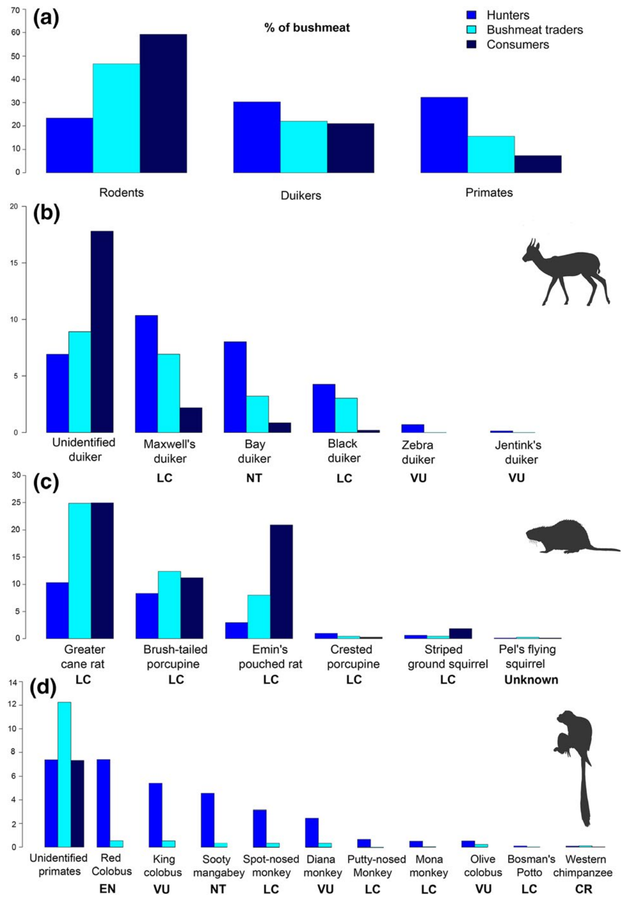

FIGURE 2 Proportional distribution of taxa and species utilized by hunters (blue), bushmeat traders (turquoise), and consumers (dark blue) in relation to the total amount of utilized bushmeat. (a) Proportional distribution of duikers, rodents and primates (b) Utilization of duikers, (c) Utilization of rodents, (d) Utilization of primates (for detailed information see Appendix Table A.2.1). Categorization by the International Union for Conservation of Nature (IUCN): Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC)

and 74.5% of the traders ($n = 161$) sold rodents. Duikers were the second highest traded taxa (22%), and 77% of traders sold duiker meat. Primates were the least traded taxa (15.6%) and around half of the traders (51.8%) reported selling primates. Correspondingly, consumers ($n = 912$) covered over half of requirements on bushmeat by rodent meat (59.2%), followed by duiker (21%) and primate meat (7.3%; Figure 2a), whilst consumers utilized primate meat the least of all user groups. Around a quarter (25.9%) of the consumers reported consuming primate meat, around half (55.7%) cited duiker meat, and nearly seventy per cent (67.7%) confirmed rodent consumption. Across all user groups, greater cane rats were the most exploited individual species (Figure 2c, Appendix Table A.2.1).

3.1 | Diversity of utilized species

The total number of different species utilized was influenced by the socioeconomic characteristics of hunters (full-null model comparison [LRT]: $\chi^2 = 36.04$, $df = 12$, $p < 0.001$) and consumers (LRT: $\chi^2 = 49.36$, $df = 10$, $p < 0.001$). For traders, we observed no noticeable effect (LRT: $\chi^2 = 11.44$, $df = 9$, $p = 0.247$; Appendix Table A.2.3). Hunters and consumers with an awareness of the depleting effects of bushmeat hunting used fewer species (Figure 3, 1a, 1c; Appendix Tables A.2.2 and A.2.4). Hunters targeted more species when they relied on bushmeat economically, and where local prices for alternative proteins from fish and livestock were low (Figure 3, 1a; Appendix Table A.2.2). The cultural factor of religion influenced consumption, with Muslims consuming the least species (Figure 3, 1c; Appendix Table A.2.4). The control predictors showed that hunters and consumers with a longer duration of residence in a settlement utilized a more diverse range of species. Moreover, where bushmeat prices were low, a greater range of species was hunted (Figure 3, 1a, 1c; Appendix Tables A2.2 and A.2.4). For information on random effects, see Appendix 4.

3.2 | Taxon-specific utilization

3.2.1 | Utilization of primates

Hunting primates was highly influenced by our test predictors (LRT: $\chi^2 = 38.79$, $df = 12$, $p < 0.001$). The cultural-related predictor, taboo had the strongest effect and hunters who adhered to a primate taboo caught 95% fewer primates. Additionally, hunters educated in environmental awareness targeted 57% fewer primates. In contrast, hunters dependent on bushmeat income hunted more primates. Additionally, in places with greater availability of alternative protein from fish and livestock, more primates were hunted. For our control predictors, we found that older hunters and hunters who spent more of their lifetime in the settlement caught more

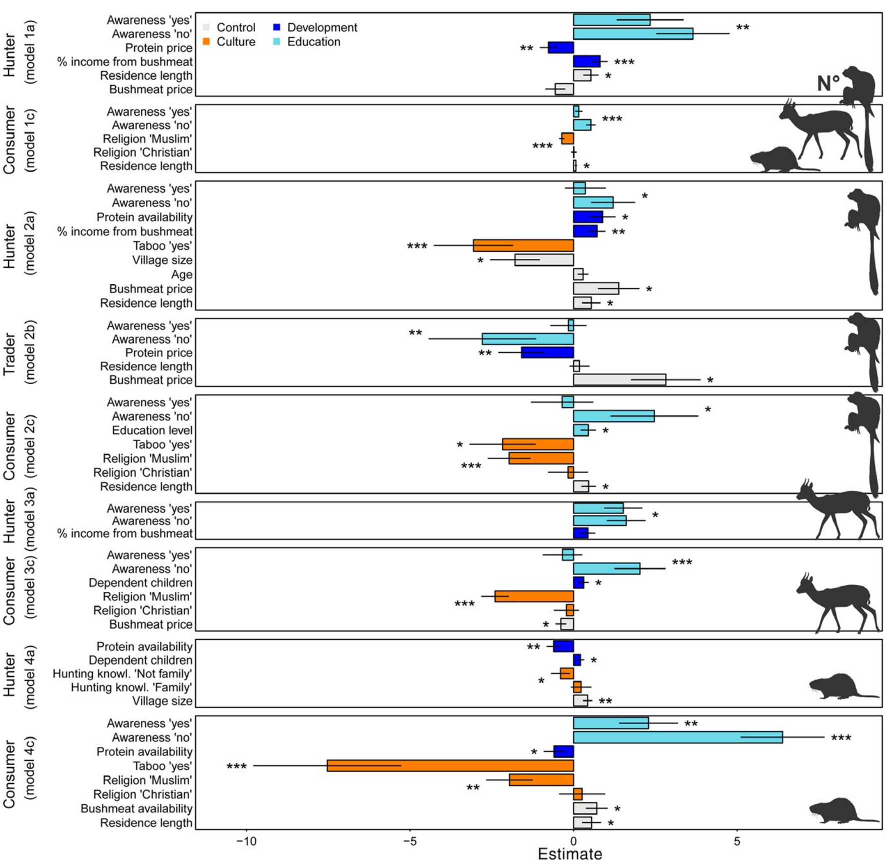

FIGURE 3 Significant fixed effects of each significant model (full-null-model-comparison, $p \leq 0.05$). Significance levels: $p > 0.05$ – < 0.10, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$. Colours depict the group of potential explanatory factors (dark blue: development-related; turquoise: education-related; orange: cultural-related); grey: control predictors). Responses variables of models were number of different species used (model 1a, 1c), number of primates hunted (model 2a), number of primates traded (model 2b), frequency of consumption of primate meat (model 2c), number of duikers hunted (model 3a), frequency of consumption of duiker meat (model 3c), number of rodents hunted (model 4a), and frequency of consumption of rodent meat (model 4c)

primates. Moreover, more primates were caught in smaller settlements, and when prices for primate meat were higher (Figure 3, 2a; Appendix Table A.2.5).

Regarding the trade of primates, we found a marginally non-significant effect of the test predictors (LRT: $\chi^2 = 14.50$, $df = 8$, $p = 0.070$). Traders who knew about the harmful environmental effects traded more primates. More primates were also sold, where local prices of alternative protein were low. The control predictors showed that traders with more of their life spent in the settlement sold more primates. Here also, more primates were marketed when prices for primate meat were high (Figure 3, 2a; Appendix Table A.2.8).

Primate meat consumers were highly influenced by the predictors (LRT: $\chi^2 = 31.45$, $df = 10$, $p < 0.001$). Environmental awareness was associated with 95% lower consumption frequencies of primate meat. The effect of religion was also substantial, and Muslims consumed 86% less primate meat than Animists. When primates were considered a taboo animal, consumption levels lowered by 89%. Consumption of primate meat was positively associated with education level. For the control predictor duration of residence, we found that consumers who had lived longer in a settlement consumed more primates (Figure 3, 2c; Appendix Table A.2.11). For information about random effects, see Appendix 4.

3.2.2 | Utilization of duikers

The number of duikers harvested by a hunter was explained well by our predictors (LRT: $\chi^2 = 20.21$, $df = 11$, $p = 0.043$). Here more economically reliant hunters targeted more duikers, and hunters with awareness about the environmental effects of bushmeat harvested 9% fewer duikers (Figure 3, 3a; Appendix Table A.2.6).

Trading duikers seemed not to be influenced by our predictors (LRT: $\chi^2 = 6.39$, $df = 8$, $p = 0.604$; Appendix Table A.2.9). Consumption of duiker meat, however, was associated with the test predictors (LRT: $\chi^2 = 59.99$, $df = 9$, $p < 0.001$). Religion strongly influenced consumption patterns, and Muslims consumed 90.6% less duiker meat than animists. Furthermore, people with environmental awareness consumed 90.8% less duiker meat. Higher consumption of duiker meat was related to the number of dependent children in a household, and its lower price (Figure 3, 3c; Appendix Table A.2.12). For information about random effects, see Appendix 4.

3.2.3 | Utilization of rodents

The number of rodents caught by a given hunter was affected by the predictors (LRT: $\chi^2 = 24.87$, $df = 12$, $p = 0.015$). Hunters with hunting knowledge transmitted through the family harvested more rodents than people who learned hunting by themselves or through peers. Additionally, hunters with more dependent children at home hunted rodents to a greater extent. Moreover, higher amounts of rodents were caught in larger settlements, and where the availability of alternative protein was low (Figure 3, 4a; Appendix Table A.2.7). The trade of rodents was not obviously influenced by our test predictors (LRT: $\chi^2 = 7.43$, $df = 8$, $p = 0.490$; Appendix Table A.2.10).

Consumption of rodents, in contrast, was clearly associated with our predictors (LRT: $\chi^2 = 78.94$, $df = 10$, $p < 0.001$). People with environmental awareness consumed 94.1% less rodent meat. Religion also had strong effects and consumption levels were 86.1% lower for Muslims compared to Animists. Furthermore, people with taboos against eating rodents consumed 88.5% less rodent meat. In settlements where proteins from fish and livestock were deficient, rodent consumption was higher. The control predictors showed that rodent meat was consumed in higher frequencies by people with longer residence in the settlement and if there was more rodent meat available (Figure 3, 4c; Appendix Table A.2.13). For information about random effects, see Appendix 4.

4 | DISCUSSION

The key finding of our study is that the different user groups of bushmeat selected species very differently. More specifically, hunting of primates and duikers was connected to economic reliance, whereas hunting and consumption of rodents were associated with higher nutritional reliance. The utilization of most taxa was related to differing levels of environmental awareness, and consumption of primate meat to a cultural and educational context. Previous studies have shown that within a commodity chain the motivations for utilization of bushmeat can vary between user groups (Bachmann et al., 2019) and the determinants of specific taxa utilization can vary within the same user group (Catarina et al., 2017; East et al., 2005; Foerster et al., 2012; Jones et al., 2018; Luiselli et al., 2019). According to our results, determinants and preferences can vary not only between and within user groups, but also depending on taxa, revealing the full complexity. Development, education and culture-based strategies may here affect different nodes in the bushmeat commodity chain differently. The largest proportions of traded and consumed animals were non-endangered rodents and duikers, and mainly hunters primarily targeted vulnerable and endangered primates and duikers (Figure 2; Appendix Table A.2.1). The observed distribution of abundant and vulnerable species matches well to descriptions from similar landscapes (Gonedelé Bi et al., 2017; Kouassi et al., 2017; Petrozzi et al., 2016; Schulte-Herbrüggen et al., 2013). Considering this extensive use of abundant species paired with the taxon-specific drivers, broad strategies to reduce trading and consumption of bushmeat may in reality address abundant taxa and fail to target rare species.

4.1 | Effects of predictors associated with development-based strategies

In our analyses, we found the strongest support for effects of economic reliance for hunters. Here hunters more dependent on bushmeat income targeted a broader diversity of species (Figure 3, 1a, 2a, 3a), probably because they preferred species-rich PAs over agricultural landscapes as hunting grounds (Bachmann et al., 2019). Furthermore, the long travel distance to and within the PAs (22.45 ± 19.88 km), and the associated risk of apprehension by park rangers may foster opportunistic behaviour, causing hunters to target any profitable species. Economically reliant hunters targeted more primates and duikers, likely because species caught by selective methods are more likely to be sold than species caught by unselective methods like traps (Allebone-Webb et al., 2011). Here consumers reported in 40% of cases to catch rodents by themselves ($n = 495$), whereas 85% ($n = 267$) of the duiker and 90% ($n = 111$) of the primate meat were purchased. Nutritional reliance on bushmeat due to low accessibility of proteins from fish and farmed meat only affected utilization of rodents (Figure 3).

Additionally, our results showed, that families with more children and resultant higher economic and nutritional requirements, hunted and consumed more rodents and consumed duiker meat more frequently, especially when it was cheap (Figure 3). Hence, duiker and rodent meat may represent an everyday source of protein for large households (Kouassi et al., 2017). Counter-intuitively, cheap and available alternative protein increased the species diversity and quantity of primates hunted. This relationship might be non-causal, as both variables can be indicators of higher market accessibility, which can facilitate the sale of bushmeat, and thus spur commercial hunting (Allebone-Webb et al., 2011; Junker et al., 2015). When assuming causality here, reducing economic reliance of hunters on bushmeat through the provision of alternative livelihoods, ideally combined with enforcement and sanctions (Bachmann et al., 2019; Sylvia & Coad, 2019), could reduce offtake of duikers and primates. However, primates were consumed independently from price and the availability of proteins, hence, providing consumers with bushmeat substitutes would probably decrease demand on rodents, but not necessarily on vulnerable species like primates.

4.2 | Effects of predictors associated with education-based strategies

Environmental awareness was an influential predictor explaining variation in most of our models. This parallels recent evidence that awareness can decrease bushmeat consumption, especially when reliance on bushmeat is assumed to be low (Bachmann et al., 2019; Kouassi et al., 2017; Morsello et al., 2015). However, the impact varied between taxa and user groups. For instance, hunters aware of the negative ecological consequences of over-hunting hunted 57% less primates, but only 9% less duikers, compared to those not aware. Conversely, according to our results, traders with environmental awareness traded higher quantities of primates. It is plausible that traders observed changes in the abundance of this susceptible taxon, yet this recognition did not result in behavioural change. Here the reliance on this income and an observed high competition between traders competing over the hunter's harvest, may not have allowed selectivity (Bachmann et al., 2019). Unexpectedly, the consumption of primate meat was associated with more years of school attendance, which contradicts other evidence. For instance, in the neighbouring country Liberia, high literacy rates were correlated with high chimpanzee densities (Junker et al., 2015) and in Gabon, people who attended school longer consumed less primate meat (Foerster et al., 2012). However, primate meat was consumed independent of its price and availability of alternatives and reliance on primate meat was low (7.2% of consumption frequencies)—factors, which may suggest luxury product consumption (East et al., 2005; Foerster et al., 2012). Hence, consumers, with higher disposable incomes or higher status would more likely consume primate meat, both of which are characteristics that would apply to educated people (ENV, 2015). Alternatively, since we found no effect of income, well-educated respondents may have picked up this habit while attending high schools in urban centres, where restaurants often offer primate meat (Caspary, 1999). In summary, education alone did not automatically lead to more pro-environmental behaviour, but environmental education may serve as the priming agent for behavioural changes when socioeconomic circumstances allow for flexibility.

4.3 | Effects of predictors associated with cultural-based strategies

Cultural habits were a strong predictor in specific taxa- and user group models. Religious affiliation affected only consumption choices, probably because of different perceptions of nature and religious prohibitions. The high consumption levels of Christians may reflect a utilitarian 'mastery-over-nature orientation' tradition, which justifies the exploitation of nature's resources for one's benefit (Gifford, 2012). Notably, protestants often mentioned that God created animals for human consumption and will thus secure its supply (Bachmann et al., 2019). Animists showed unexpectedly high consumption rates, as this religion is usually associated with local resource management mechanisms and a mutualism value orientation, in which wildlife deserves care (Gifford, 2012). The large-scale migration in the Taï region (ENV, 2015) may have fostered non-adherence to local traditions (Golden & Comaroff, 2015a). Muslims consumed the least bushmeat across all taxa. This matches findings from Sierra Leone, where Muslims shunned certain species like wild boar, snakes, primates and rodents forbidden by Quran law as '*haram*'. However, this was no reason to not kill and sell them (Bonwitt et al., 2017). Here many Muslims also avoided animals not slaughtered by *halal* stipulations, which applied to most animals shot in PAs. Moreover, consuming less bushmeat can also be connected to the belief that humans have a role in responsible leadership of life created by Allah (Gifford, 2012). Traditional taboos forbid hunting and consumption of primates and consumption of rodents, mirroring results from Sierra Leone (Bonwitt et al., 2017) and Madagascar, where many taboos centred on primates like lemurs, (Golden & Comaroff, 2015a, 2015b). A threat to this environmentally friendly habit is the missionary work of evangelist churches (Golden & Comaroff, 2015a), which have also in the Taï region influenced people to abandon their taboos (Bachmann et al., 2019). Hunters with traditionally transmitted hunting knowledge targeted more rodents, which could support our hypothesis of more sustainable resource use by traditional hunters.

It could also reflect family traditions including knowledge about how to build and place successful traps for rodents. Overall, these multiple traditional habits, potentially promoting sustainability, enable combined culture-based strategies. The reinforcement of taboos and traditional hunting knowledge could improve primate conservation, and a dialogue between churches and conservationists could exploit the full potential of environmental concerns rooted in religious beliefs and values.

4.4 | Pathways towards sustainability

Conservation problems are also behaviour change problems, and thus the development of sustainable pathways require identification of the behaviour of interest, the key actors and the underlying baseline conditions, as well as information on alternative behavioural mechanisms and success of interventions (Reddy et al., 2017). Generally, substituting bushmeat utilization entirely by fish and livestock would have negative collateral impacts. Substituting one tonne of bushmeat by local beef requires approximately 6.25 ha of pasture and would lead to habitat conversion (Nasi et al., 2011). Notably, none of the heavily used rodent species, but two less utilized duiker species and five frequently used primate species were threatened (Figure 2). Handling of phylogenetically similar species like primates involves risks of zoonosis infections or spillover (Olival et al., 2017). Rodents, especially in highly human-populated areas, can also constitute a disease risk (Olival et al., 2017). Despite this, rodents can contribute to food security, which can decrease the diversity of bushmeat species utilized and hence, the additional exposure to reservoirs of novel pathogens from other species (Friant et al., 2020). Overall, rodents may provide a comparably sustainable source of protein, while the situation for primates is critical. Hence, the behaviour in question, at least from a conservation perspective, is the utilization of primates. Regarding the actors involved, a successful regulation of the bushmeat trade requires targeting interventions at the optimal node in the commodity chain (Bachmann et al., 2019). To limit the use to the resilient taxon, hunters will bear the highest costs of not shooting at-risk species, increasing their foraging time (Brown & Robinson, 2003) and hence, the risk of detection. Additionally, hunters highly depended on profit from primates (32.3%; Figures 2 and 3) and made greater investments to reach wildlife-rich hunting grounds. The low selectivity of traders may also indicate high costs of rejecting species, although primates only constituted 16% of their stock (Figure 2). Consumption, however, was shaped by multiple factors, indicating low costs of selectivity (Figure 2). For instance, although Muslim hunters did not forgo profits in hunting primates, Muslim consumers shunned primate meat (Figure 2). While high prices of primate meat encouraged traders to sell, and hunters to poach primates under high risk, consumption was price-independent (Figure 3). Usually, as long as consumers are willing to pay a premium price for certain species, there will be hunters and traders willing to link supply and demand (Brown & Robinson, 2003).

Consequently, consumers may present here the key node for interventions (Bachmann et al., 2019). Several conditions can increase the success of demand-reduction approaches. This includes low reliance (Bachmann et al., 2019), especially on primate meat (7.2%), and prevailing cultural norms and ethical and moral beliefs (Bachmann et al., 2019), triggering avoidance of primates. These are self-enforced by social norms or internalized, and independent from frequently difficult implementation of law enforcement (Colding & Folke, 2001; Kablan et al., 2017). For instance, for urban Amazonian residents, cultural taboos were more relevantly deterrent against bushmeat consumption and trade than weakly enforced laws (Morsello et al., 2015). Additionally, reinforcement of existent ethical and moral convictions can trigger intrinsic incentives for conservation, which increase perceptions of self-efficacy, acting beneficially on pro-environmental behaviours (Clayton, Litchfield, & Geller, 2013; Reddy et al., 2017). In particular, taboos and environmental awareness bear the potential for large-scale change by campaigns communicating traditional, ethical, moral, environmental and health-related issues such as risks of zoonosis transmission through primates (Olival et al., 2017). For instance, in Liberia, households consumed bushmeat less frequently if they knew that Ebola could be contracted from bushmeat (Ordaz-Németh et al., 2017). There are more encouraging examples, including a drastic decline in shark fin sales in China after implementing large-scale and well-designed culturally sensitive and celebrity-driven multimedia campaigns (Whitcraft et al., 2014). Nevertheless, a market reduction-driven approach must consider cascading effects and offer livelihood alternatives for groups dependent on bushmeat, like hunters or traders (Bachmann et al., 2019). In summary, consumer-level interventions through cultural- and educational-based campaigns tailored explicitly to endangered species may offer the most promising strategy towards sustainability.

4.5 | Study limitations

Studies investigating pro-environmental behaviours often have to rely on self-reported behaviour, which can deviate from the actual behaviour due to imperfect memory, social desirability bias or fear of persecution (Gifford, 2012). We therefore applied several precautionary measures (Appendix 1.2). However, three potential effects described in the literature, could bias our dataset: (a) respondents may over- or underestimate true resource utilization (Gavin et al., 2009; Golden et al., 2011), which would bias the intercepts of our models; (b) people over-report low levels and under-report high levels of exploitation (Jones et al., 2008), which would decrease the magnitude of the estimated effects (i.e. the slopes) and ultimately the power of our analyses; (c) random errors due to imprecise memory (Gavin et al., 2009; Golden et al., 2011), which also would hamper the detection of effects. However, in all these three scenarios, we expect a higher likelihood of false-negative, but not false-positive results. Furthermore, people tend to underestimate common, and overestimate the frequency of rare events (Golden et al., 2011).

Therefore, the utilization of abundant species may in reality, be higher, and the use of rare species and taxa, lower (Figure 2). This may explain the comparably high catch frequencies of the rare red colobus *P. badius* (Figure 2). Hence, proportions should be treated with some caution, even when they match well to descriptions from similar landscapes (Gonedelé Bi et al., 2017; Kouassi et al., 2017; Petrozzi et al., 2016; Schulte-Herbrüggen et al., 2013). Overall, we expect the systematic bias to be minimal because our estimates of primate utilization closely match those of another study from this region (Kouassi et al., 2017).

Furthermore, basing data collection on hunters' annual catch recall has been found to diminish bias due to rare events and seasonal variation and performs better than recall of the previous month (Golden et al., 2011). Also, annual and punctual interviews determining bushmeat traders' perceptions of quantity sold and the price have been shown to be accurate (Mayor et al., 2019). Additionally, respondents report regularly performed tasks with higher accuracy, especially when they do not fear legal prosecution, and personal attributes like education are not related to higher accuracy levels or to biased responses (Gavin et al., 2009; Golden et al., 2011; Jones et al., 2008; Mayor et al., 2019). However, complex underlying psychological mechanisms exacerbate the difficulty of disentangling causalities and require further research. For instance, frequent bushmeat users could be more likely to deny environmental impacts to justify their behaviour. Despite these potential caveats, the dataset seems suitable to answer our research question and provides detailed insights into the usually hidden wildlife trade.

4.6 | The need for differentiated research and conservation approaches

Groups with shared characteristics favoured similar taxa and different groups used the same taxon for varying reasons. Consequently, these groups may differ in their responsiveness to development-, education-, and culture-based approaches (Jones et al., 2018). Social marketing techniques like audience segmentation can help to lump together individuals with a similar background to increase cost-efficiency of interventions (Jones et al., 2018). Likewise, if messages are disadvantageously framed or broadcast too widely, no one may feel addressed or, worse, campaigns may backfire (Reddy et al., 2017). For instance, bushmeat reduction campaigns including widespread species, resting on a conservation argument may lose their credibility, or addressing and describing large numbers of people carrying out environmentally destructive behaviours can normalize and paradoxically encourage these behaviours (Reddy et al., 2017). Hence, to change a specific behaviour, it is essential to define a clear target audience and the behaviour in question, and the motives of the audience performing it must be understood (Clayton et al., 2013; Reddy et al., 2017). Surprisingly, prior baseline data collection in projects aiming to reduce hunting is not very common throughout West and Central Africa (Sylvia & Coad, 2019). Knowledge and tools from psychological science can help here to appropriately frame messages and identify barriers to, and benefits of the promoted behaviour, which facilitates campaigns to best fit individual's existing lifestyles rather than the other way around (Clayton et al., 2013; Reddy et al., 2017).

5 | CONCLUSION

Overall, the divergent pressures operating at each node of the commodity chain highlight the diverse, multifaceted, nuanced and complex relationships between bushmeat and its users, and explain the observed challenge to successfully regulate the bushmeat trade. Hence, there exists no one-size-fits-all solution and we urge higher prioritization of planning processes and a stronger focus on user groups and taxa in conservation strategies and research. Community-driven solutions can help here to adapt to diverse contexts and can additionally foster beneficial self-motivation for conservation (Clayton et al., 2013; Friant et al., 2020). Ultimately, a deeper understanding of specific resource use, the definition of clear conservation goals, prior in-depth research to identify the targets and appropriately tailored conservation activities around these are the most important pathways for successful solutions to the bushmeat crisis.

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CONFLICTS OF INTEREST

The authors have no competing interests to declare.

AUTHORS' CONTRIBUTIONS

M.E.B., the first author, developed the research idea and study set-up, organized and lead the data collection, conducted the analyses and had the lead on writing the manuscript. H.S.K. supervised the manuscript of the PhD candidate M.E.B. He supported the design of the methodology, the analyses and the writing phase by constant supervision and intellectual input; J.A.K.K. established the infrastructure for the field work and gave practical advice, as well as intellectual contribution during the planning phase, the questionnaire design, data collection and writing process; R.M. supported the statistical analyses and interpretation of the data, and gave methodological and conceptual advice during all phases of processing; M.R.N., H.C. and D.H. provided critical and well thought through intellectual input during drafting the manuscript, the writing process and all revisions of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are publicly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.9ghx3fff7 (Bachmann et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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