Species misidentification in local markets: Discrepancies between reporting and molecular identification of bushmeat species in northern Uganda

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ABSTRACT

 Bushmeat hunting and consumption, although widely utilized as necessary supplement to household income and nutrition in many regions, presents threats to public health and wildlife conservation efforts. In northern Uganda, consumption of bats and primates, two wildlife groups often implicated in zoonotic disease emergence, is not widely culturally accepted; however, these species are reported by hunters to often be hunted and sold as culturally desirable species, like antelope and warthog. To investigate the prevalence of market bushmeat misidentification, we collected 229 bushmeat samples from 23 communities adjacent to Murchison Falls National Park. Reported species was recorded on acquisition for each sample. PCR targeting mammalian cyt b and 12 s rRNA genes and sequencing were performed to identify samples to the lowest taxonomic unit using NCBI BLAST. Overall, 27.9% (61/219) of samples had disparate results between species reported and BLAST analysis. Thirty-four species were identified, with the most frequent wildlife being waterbuck (31.5%), warthog (13.7%), and black rat (5.9%). These data reveal a public health risk for bushmeat consumers in northern Uganda as they cannot assess species-related risk when purchasing bushmeat and take appropriate precautions against zoonotic pathogen exposure. These data also provide insight into regional hunter prey preference and market preference of local community members which may inform conservation strategy in the region.

1. Introduction

Bushmeat harvest and consumption is a well-described practice in sub-Saharan Africa and plays an important role in food security and nutrition, income security, and crop protection, particularly in rural communities [1–3]. However, even within the framework of economic provision, the issue of bushmeat harvest presents two major concerns: the public health risk to communities through exposure to zoonotic pathogens and threat to the conservation of protected wildlife species. Since the 1970s, over 60% of emerging infectious diseases affecting human populations have been zoonotic in nature, with 71.8% of those zoonotic events resulting from contact with wildlife species [4]. Within the last several decades, Uganda has reported numerous zoonotic disease events resulting from contact with wildlife species, including anthrax, Ebola virus, Marburg virus, rabies virus, yellow fever, and HTLV/STLV-1 [5–7]. Certain wildlife species have historically been identified as having higher inherent risk of zoonotic disease emergence, particularly bats, non-human primates (NHPs), ungulates, and rodents [8].

Quantification of bushmeat harvest has been described for some sub-Saharan African countries, particularly those in West and Central Africa. Estimates for Nigeria and Cameroon [9], Ghana [10], Cote d’Ivoire [11], and the Congo Basin [12,13] range from 12,000 tons to 4.9 million tons annually; however, few reports are available for Uganda [14]. Murchison Falls National Park in northern Uganda is the oldest and largest protected area in Uganda and is renowned for its biodiversity. Wildlife species within the park are highly susceptible to hunting as many of the park’s borders are directly adjacent to local communities, increasing potential for human conflict with wildlife, as well as increased opportunity and incentive to hunt.

In Uganda, all hunting of wildlife species is illegal except for vervet monkeys (Chlorocebus pygerythrus), olive baboons (Papio anubis), and bushpigs (Potamochoerus larvatus) [15,16]. Hunting of these species is permitted without penalty under the supervision of the Uganda Wildlife
Authority when they are found to depredate crops [17]. Despite the legal restrictions on hunting, bushmeat harvesting is a common and an accepted practice, with meat being used for both food and sold locally as an additional source of income. During preliminary communications, hunters claimed to conduct and be aware of ‘species misrepresentation’ at market, where species that were culturally unacceptable to consume (like NHPs) were opportunistically hunted and disguised and sold as culturally desirable/acceptable species, such as antelopes, warthogs, and bushrats (Willcox - personal communications, 2016). Due to the clandestine nature of bushmeat hunting in Uganda there are no markets where carcasses are openly displayed for purchase to the consumer, but rather transactions occur person-to-person – often with meat already butchered [18].

We hypothesized that species misrepresentation does occur in the bushmeat market in northern Uganda. This study aims to describe the most frequently hunted species and quantify rates of species misidentification in markets to identify potential opportunities for increased risk of contact-based and foodborne zoonotic infections.

2. Methods

2.1. Study area

Samples were collected from 22 villages within the Nwoya district in northern Uganda (Fig. 1). The Nwoya district is composed of 4 sub-counties, Purongo, Anaka, Alero, and Koch Goma, and it forms the northern border of the Murchison Falls Conservation Area (MFCA). The MFCA is Uganda’s largest continuous protected area, consisting of the 3893 km² Murchison Falls National Park (MFNP) to the north, the 748 km² Bugungu Wildlife Reserve (BWR) to the southwest, and the 720 km² Karuma Falls Wildlife Reserve (KFWR) to the southeast. Villages where bushmeat samples were collected are shown in Fig. 1.

2.2. Sampling

Initial contact with hunters and dealers in the communities were made through Ugandan community liaisons and research associates. Bushmeat samples were purchased from hunters, dealers, and women within study communities from July to August 2016 and from June to July 2017 for the price of 10,000 Ugandan shillings (equivalent of approximately $3 US) per sample. Species reported, condition of meat (fresh, smoked, hard-smoked), and village where purchased were recorded for each sample. Tissue was considered fresh when harvested from bushmeat and no treatment of meat was applied other than storage. Tissue was considered smoked if the meat was harvested and noted to be smoked but was soft and the internal portion was differently textured and colored. Tissue was considered hard smoked if the meat was smoked, hard to the touch, and homogenous in texture and color. Once collected, an interior section of each bushmeat tissue was excised using a sterile scalpel blade. Samples from 2017 (91–226) were placed immediately into RNALater™ Stabilization Solution (Thermo Fisher Scientific) in sterile Eppendorf conical tubes to preserve the genomic DNA and RNA due to additional funding that allowed for viral sequencing. Samples were 2016 (1–90) were placed in sterile Eppendorf conical tubes. All samples were stored in 18°C freezers in Gulu, Uganda immediately after collection and transported to Makerere University, Kampala on ice for long-term storage at –80°C.

2.3. Molecular techniques

DNA extraction was performed on all samples using the DNeasy® Blood & Tissue Extraction Kit (QIAGEN) according to manufacturer’s instructions. The success of DNA extraction was confirmed by gel electrophoresis on 2% agarose. A polymerase chain reaction was performed on extracted DNA using two universal mammalian primers and cycling conditions summarized in Table 1. MTCB-F/MTCB-R universal mammalian primers targeting the mitochondrial cytochrome b gene were used first (Naidu et al. 2012). If this procedure was unable to

Fig. 1. Map of Murchison Fall Conservation Area and Adjacent District (A) Map of Africa showing the location of Uganda and Murchison Falls Conservation Area (MFCA), and (B) Nwoya District and its sub-counties (black hatched area) and the MFCA protected area (dark green area) Murchison Falls National Park (MFNP), Bugungu Wildlife Reserve (BWR) and Karuma Falls Wildlife Reserve (KFWR) with the major highways (red line) and sub-counties. Blue dots represent general areas from which samples were obtained. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
provide clean sequences, L1085/H1259 universal vertebrate primers targeting the 12 s rRNA gene were used (Kitano et al. 2007) instead. Gel electrophoresis was performed on all PCR products on a 2% agarose gel stained with ethidium bromide. PCR products were purified using QIAquick® PCR Purification Kit (QIAGEN) according to manufacturer’s instructions. Purified PCR products were sent to Macrogen, Inc. for Sanger sequencing. The overlapping ends of the forward and reverse strands were aligned using chromatograms in Sequencher 5.46 software (GeneCodes Corporation) to create a consensus nucleotide sequence. Resultant consensus nucleotide sequences were entered into National Center for Biotechnology Information (NCBI) Basic Local Alignment Search Tool (BLAST) to identify mammalian species to the lowest possible taxonomic unit.

2.4. Analysis

BLAST results were compared to species reported by bushmeat providers at point of sale to calculate the crude rate of mismatch within our samples. Discrepancy was coded as 0 (no mismatch) if the molecular results matched to species level or if reported species and molecular result were within the same clade. For example, if “kob” was reported but the molecular result was waterbuck, both are antelope species and no discrepancy was recorded. Species were coded as 1 (mismatch) if reported species results did not match to species level and were not within the same clade.

Comparison of proportions of discrepancy among bushmeat source groups was performed in SPSS® using the Bonferroni method. These results were confirmed with a two-sided test of proportions (pretest function) using STATATA®. Logistic regression was performed with discrepancy as the binary outcome variable and sample source, village, and molecularly identified species as predictor variables using IBM SPSS version 25.

3. Results

3.1. Sample collection

Bushmeat samples (n = 229) were collected from 22 communities. Eighty-nine samples were collected in 2016 and 140 in 2017. Samples were obtained from villages within Anaka, Koch Goma, and Purongo sub-counties. 127 (58%) samples were provided by hunters compared to dealers (n = 37; 16.9%) or cooks (n = 55; 25.1%). These data are shown in Table 2. Data on species reported by sample source are shown in Table 3. Thirty-eight different species were reported by bushmeat providers, with two samples reported as “unknown bushmeat species.” Kob was the most frequently reported species (n = 63; 28.8%). Only seven samples were reported as vermin species, including baboon (n = 5), bushpig (n = 1), and vervet monkey (n = 1). The condition of bushmeat samples ranged from fresh to hard-smoked, with 112 (48.9%) fresh, 104 (45.4%) smoked, and 13 (5.7%) hard-smoked.

3.2. Molecular results

Ten samples were omitted from final analysis due to degraded tissue from excessive smoking, resulting in 219 viable samples. Consensus sequences ranged from 85 to 918 bp in length, and molecular results are summarized in Table 4. Thirty-four different species were identified using NCBI BLAST. One sample could only be identified to genus level.

### Table 1

| Primer | PCR product size (bp) | Primer Sequence 5’ to 3’ | DNA Target | Cycling Conditions | Reference |
|--------|-----------------------|--------------------------|------------|--------------------|----------|
| MTCB-F | 1420                  | CCHCATAAATAGGNGAAG       | cyt b      | 95°C/45 s, 55°C/60 s, 72°C/2 min, 35 cycles | Naidu et al. 2012 |
| MTCB-R | 1420                  | WAGAAYTTCCAGCTTTGG       | cyt b      | 95°C/45 s, 55°C/60 s, 72°C/2 min, 35 cycles | Naidu et al. 2012 |
| L1085  | 215                   | CCCAAAATCGGATAGTATACCC   | 12S rRNA   | 94°C/30 s, 55°C/30 s, 72°C/30 s, 35 cycles | Kitano et al. 2007 |
| H1259  | 215                   | GTTTGCTGAAAGATGGGGTGA    | 12S rRNA   | 94°C/30 s, 55°C/30 s, 72°C/30 s, 35 cycles | Kitano et al. 2007 |

### Table 2

| Source   | Number and percentage of samples provided | Number and percentage of correctly identified samples using molecular typing |
|----------|------------------------------------------|--------------------------------------------------------------------------|
| Hunter   | 127 (58%)                                | 81 (63.8%)                                                              |
| Women    | 55 (25.1%)                               | 45 (81.8%)                                                              |
| Dealer   | 37 (16.9%)                               | 33 (92.2%)                                                              |
| Total    | 219 (100%)                               | 159 (72.6%)                                                             |

Subscripts denote proportions of accurately identified samples by source that do not differ significantly from each other at a 0.05 significance level using the Bonferroni method. P = 0.002.
Identity of samples to first BLAST result ranged from 90% to 100%. The most frequently identified species by molecular methods was waterbuck (*Kobus ellipsiprymnus*), with 69 samples (31.5%). In total, 108 (49.3%) samples were antelope species. Only 3 samples were found to be one of the three legal species to hunt: 2 olive baboons and one bushpig. Twenty-three (10.5%) of the samples were found to be domestic species (cow, goat, and sheep).

### Table 4

| Scientific Name | Common Name | Number (n) and Percentage (%) of Total Bushmeat Samples | Number (n) and Percentage (%) of Correctly Identified to Correct Species |
|-----------------|-------------|--------------------------------------------------------|------------------------------------------------------------------------|
| *Kobus ellipsiprymnus* | Waterbuck | 69 (31.5%) | 61 (88.4%) |
| *Phacochoerus africanus* | Common warthog | 30 (13.7%) | 24 (80.0%) |
| *Capra hircus* | Domestic goat | 14 (6.4%) | 0 (0%) |
| *Rhinoceros burchellii* | Black rhino | 13 (5.9%) | 8 (61.5%) |
| *Kobus leche* | Lechwe | 11 (5.0%) | 11 (100.0%) |
| *Kobus kob* | Kob | 9 (4.1%) | 9 (100.0%) |
| *Hippopotamus amphibius* | Hippopotamus | 8 (3.7%) | 6 (75.0%) |
| *Bos taurus* | Domestic cow | 7 (3.2%) | 0 (0%) |
| *Oryx dammah* | Grey oryx | 3 (1.4%) | 2 (66.7%) |
| *Genetta taurinus* | Tawny genet | 5 (2.3%) | 3 (60.0%) |
| *Syncerus caffer* | Blue wildebeest | 4 (1.8%) | 2 (50.0%) |
| *Lepus timidus* | African savanna hare | 4 (1.8%) | 1 (25.0%) |
| *Ourebia ourebi* | Oribi | 4 (1.8%) | 4 (100.0%) |
| *Pelea capreolus* | Grey reedbuck | 4 (1.8%) | 4 (100.0%) |
| *Chlorocebus aethiops* | Tantalus monkey | 3 (1.4%) | 1 (100.0%) |
| *Hystrix cristata* | Crested porcupine | 1 (0.5%) | 1 (100.0%) |
| *Phacochoerus africanus* | Guinea gerbil | 2 (0.9%) | 1 (50.0%) |
| *Oryctolagus cuniculus* | Hartebeest | 1 (0.5%) | 1 (100.0%) |
| *Cephalophus natalensis* | Minor epauletted fruit bat | 2 (0.9%) | 1 (50.0%) |
| *Ovis aries* | Domestic sheep | 2 (0.9%) | 0 (0%) |
| *Papio anubis* | Olive baboon | 2 (0.9%) | 2 (100.0%) |
| *Tatera guinea* | Guinea gerbil | 2 (0.9%) | 1 (50.0%) |
| *Alcedo atthis* | Hartebeest | 1 (0.5%) | 1 (100.0%) |
| *Cephalophus silvicultor* | Yellow-backed duiker | 1 (0.5%) | 1 (100.0%) |
| *Chacma choeropsis* | Little free-tailed bat | 1 (0.5%) | 1 (1000%) |
| *Epomophorus gambianus* | Gambian epauletted fruit bat | 1 (0.5%) | 0 (0%) |
| *Felis sylvestris* | Wildcat | 1 (0.5%) | 0 (0%) |
| *Hyaena crocuta* | Crested porcupine | 1 (0.5%) | 1 (100.0%) |
| *Madoqua kirkii* | Kirk’s dik dik | 1 (0.5%) | 1 (100.0%) |
| *Mastomys spp.* | Multimammate mouse | 1 (0.5%) | 1 (100.0%) |
| *Mesocercomys fayra* | Greater false vampire bat | 1 (0.5%) | 1 (100.0%) |
| *Orycteropus afer* | Aardvark | 1 (0.5%) | 1 (100.0%) |
| *Reduncus arundinum* | Southern reedbuck | 1 (0.5%) | 1 (100.0%) |
| *Sus scrofa* | Bushpig | 1 (0.5%) | 0 (0%) |
| *Tatera leucogaster* | Bushveld gerbil | 1 (0.5%) | 0 (0%) |
| **Total** | **219 (100%)** | **158** | **119 (79.6%)** |

3.3. Statistical analysis results

The overall rate of species discrepancy/misrepresentation among samples was 27.9%, with 61/219 samples not matching what was reported based on sequencing. Samples acquired from hunters had the highest rate of discrepancy among the three sources of bushmeat with 36.2% being misrepresented. Women and dealers did not significantly differ from each other in proportions of discrepancy, but hunters differed significantly from both women and dealers in proportions of misrepresented samples (p = 0.002) (Table 2). No predictor variables were found to be significant in the logistic regression model.

4. Discussion

Incorrect identification of bushmeat species intended for human consumption raises a potential public health issue because it subverts the ability of bushmeat consumers to be informed about what they are handling and consuming. For example, most bushmeat consumers living in our study area should have limited contact with primates or bats, as it is culturally unacceptable to eat these animals. However, when bushmeat species misrepresentation occurs at market, these animals may infiltrate the food supply. Additionally, accurate knowledge of the species purchased may lead to differences in the degree of precautions used to prepare different meats, and therefore might lead to increased exposure to zoonotic pathogens.

Certain species are considered to carry an inherently higher risk for cross-species transmission of zoonotic pathogens, including bats, rodents, ungulates, and non-human primates [8]. A recent study indicates that community members in Nwoya district are aware that certain species carry zoonotic pathogens and may present greater risk of zoonotic disease transmission than others; therefore, the phenomenon of species misrepresentation at market may hinder the effectiveness of targeted educational efforts of safe handling and cooking of wild meats if consumers are misled about the species they are handling [18]. Hunting, butchering, cleaning, and cooking of meat places handlers in direct contact with tissue and fluids from wildlife where they may be exposed to zoonotic organisms. In 2017, the government of Uganda collaborated with the Global Health Security Agenda to identify seven priority zoonotic diseases: anthrax, influenza viruses, brucellosis, viral hemorrhagic fevers, plague, and rabies; each of these can be transmitted through contact with wildlife hosts [19].

Over a quarter of bushmeat samples included in this study were sold as a species that was not the true harvested species. There are several potential explanations for this finding. One explanation is that hunters and dealers may not know or remember which species was harvested at the point of sale. Increased efforts by the Uganda Wildlife Authority (UWA) to patrol for and prevent hunting activity has forced the harvest and sale of bushmeat to become increasingly furtive [17]. Anecdotal evidence collected from hunters in the field suggests that some of the misrepresentation observed in this study may not be intentional deception to consumers, but rather the result of efforts to hide hunting activity while in the field. Several hunters reported that when wildlife is successfully captured, the carcasses are quickly butchered in the field in such a way that the bones may be discarded and left behind [18]. This practice is performed so that hunters are less likely to be implicated if caught by UWA officers.

An alternative explanation for this rate of species misrepresentation is the intentional disguise of meat to match market demand and increase profit. Although guns were a prominent tool used in hunting during a report in 1984 [20], the domestic conflict and insurgency in Northern Uganda from the mid-1990s to 2006 fortified the ban on civilian owned firearms, forcing a greater dependence of hunters on non-specific hunting methods, like snares or pitfall traps. These hunting methods likely result in the capture of non-target bushmeat species for which there is poor market demand. This could, in turn, increase the motivation to misrepresent the species of bushmeat.
Our finding that bushmeat hunters have a lower proportion of correct sample identity than cooks and dealers (who had statistically similar proportions) are contrary to the findings in bushmeat from the Serengeti, which reported that samples collected from hunters had the greatest identification accuracy [21]. This may be due to the differences in butchering practices between sites, the variation in law enforcement, and the perceived severity of consequences if caught. For example, in Tanzania, a game cropping strategy was introduced to the Serengeti that provided legal bushmeat to villages bordering the park, attempting to decrease illegal hunting activity and to allow for increased transparency in the bushmeat market [22].

In addition to public health and emerging zoonoses concerns, conservation concerns surrounding the practice of unregulated bushmeat harvest include the decline or extirpation of wildlife species, which has been documented in several countries [23–25]. In northern Uganda, the illegality of firearms has also led to increased use of opportunistic harvest practices and non-specific capture methods. While this may decrease the frequency of hunting large-bodied wildlife, which are most vulnerable and often present in the fewest numbers, and documented to be preferred as prey by hunters, it presents difficulty in predicting which species may be most at risk from bushmeat-related activities [26]. Although bushmeat harvest may be locally sustainable in some areas, extra-local demand for bushmeat and unregulated harvest increase pressures on the wildlife populations in protected areas [21]. The over-exploitation of species geographically confined to protected areas not only threaten the survival of the species but may also increase the density of infectious diseases in wildlife populations, including endemic zoonotic diseases, facilitating their emergence in human populations who encounter these wildlife [27,28].

Our findings in this study are consistent with previous reports of commonly poached species within MPCA [14,20]. All but one of the species identified in this study are currently listed with the International Union for Conservation of Nature as “Not Threatened” (NT) or “Least Concern” (LC). Only one species (hippopotamus) is currently listed as vulnerable, and no species are listed as endangered or critically endangered. Molecular identification of animal tissue confiscated from apprehended poachers may serve as a useful tool to monitor ongoing trends of which species are most frequently hunted and may serve to inform wildlife conservation strategies.

In this study, 229 samples were obtained in the field, but ten of these samples were unable to yield readable DNA sequences. Each of these 10 samples were “smoked” and likely had DNA of compromised and degraded quality. Additionally, the collection of bushmeat samples was not performed year-round. There may be differences in the most hunted species based on seasonality. Due to the restricted sampling periods of late summer for both years, these potential differences were not identified in this study.

Four samples indicated blue wildebeest (Connochaetes taurinus) as the first sequence match through BLAST; this species does not have a geographic range in Uganda. Identity of these matches ranged from 92% to 100%. All samples whose first BLAST result was wildebeest were analyzed using the L1085/H1259 primer set. This primer set uses a shorter target sequence than the MTCB primers, which yielded higher success during PCR with samples that were more heavily smoked. However, the shorter target sequence may result in a less specific BLAST success during PCR with samples that were more heavily smoked. It is likely that these samples were wildebeest, which have a natural range in Uganda, and these four samples were not excluded from analysis.

Molecular analysis showed that 25 of our bushmeat samples were tissue of domesticated animals commonly found on subsistence farms in the area. It likely that locals provided samples of already-butchered domestic meat to community liaisons after learning through word of mouth that researchers were offering compensation for bushmeat samples. Although it is possible these samples were sold misleadingly to researchers to obtain compensation offered, we cannot exclude the possibility that the domesticated species found in this study were also being sold to community members as bushmeat. Bushmeat has been documented to be more expensive than domestic meats in market, a finding that was confirmed to be true in our study area as well [18,22,29,30].

5. Conclusions

The findings in this paper underscore the potential risks for unknown exposure to potential zoonotic pathogens. Not only do our findings confirm the widespread bushmeat trade within sampled communities, but they also demonstrate the unrecognized issue of market misrepresentation of species to consumers of hunted wildlife. The findings in this paper may establish the need for further surveillance of bushmeat trade in areas with similar regulations and social norms. Targeted educational programs focused on safe handling and food safety practices with wild animal tissues may be indicated to reduce exposure to infected tissue and to increase the appropriate precautions taken during food handling and preparation. Furthermore, molecular identification of frequently hunted and sold wildlife species provides useful information in the interest of conservation and may serve to inform strategies intended to protect these populations.

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Declaration of interest

None.

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