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Illegal bushmeat hunters compete with predators and threaten wild herbivore populations in a global tourism hotspot

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ABSTRACT

Illegal bushmeat hunting is a global threat to wildlife, but its secretive and unregulated nature undermines efforts to mitigate its impacts on wildlife and wildlife-based industries. We investigated the scale of illegal bushmeat hunting in the Okavango Delta, Botswana (~20,000 km^2) to assess its potential contribution to wildlife population declines. Approximately 1,800 illegal hunters each harvest an average of 320 kg of bushmeat annually, though some reported harvesting ≥ 1000 kg. While impala were the most commonly hunted species, buffalo and greater kudu accounted for most bushmeat. Hunters remove ~620,000 kg of medium-large herbivore biomass (equivalent to 15,500 impala) annually from the delta and humans are the fourth most prominent predator in the delta. Cumulative harvest by humans and other predators likely exceeds the intrinsic population growth rate of several species of ungulates in the delta, and helps explain purported declines in ungulate populations. Competition between humans and other apex predators for limited prey reduces the ecosystem's carrying capacity for large carnivores. Illegal bushmeat hunting represents an economically inefficient use of the delta's wildlife and a threat to the region's tourism industry. Strategies are required that provide clearer avenues for communities to benefit legally from wildlife, while concurrently curbing illegal hunting through effective law enforcement.

1. Introduction

Hunting wild animals to consume or sell their meat ("bushmeat hunting") is one of the most intensive and extensive threats to wildlife in African protected areas, with ecological and economic consequences (Lindsey et al., 2017). Bushmeat hunting drives declines in wildlife that locally extirpate populations and threaten many species with extinction (Brashares et al., 2004; Hilborn et al., 2006; Ripple et al., 2015, 2016; Harrison et al., 2016). Hunting pressure and corresponding wildlife declines are typically most severe close to human settlements or reserve boundaries (Henschel et al., 2011; Lindsey et al., 2011a; Mgawe et al., 2012; Koerner et al., 2016). Where hunting is most intensive, however, negative impacts permeate even large protected areas (Kiffner et al., 2013; Midlane, 2013). Other impacts from bushmeat hunting include skewed sex ratios and altered community composition (Holmern et al., 2006; Marealle et al., 2010; Koerner et al., 2016). These outcomes, coupled with non-lethal effects such as increased prey vigilance and altered habitat use, induce secondary population impacts (Setsaas et al., 2007; Marealle et al., 2010). By disproportionately killing rare species (Martin et al., 2013), bushmeat hunting affects vulnerable species most.

The impacts of bushmeat hunting extend far beyond species targeted for bushmeat. Indiscriminate hunting methods such as snaring kill non-target species (Becker et al., 2013). By removing prey, bushmeat hunting limits the abundance and distribution of apex predators, and thus their ecological role. (Henschel et al., 2011; Ripple et al., 2014). Excessive hunting drives trophic cascades, which

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Nomenclature

CBNRM	Community-based Natural Resource Management
DWNP	Department of Wildlife and National Parks
EWB	Elephants Without Borders
MGR	Moremi Game Reserve
NGO	Non-governmental organization
WMA	Wildlife Management Area

disrupt ecosystem processes and services (Abernethy et al., 2013; Galetti and Dirzo, 2013). Handling bushmeat increases risks of disease spillover to humans and livestock (Karesh and Noble, 2009; Kock et al., 2009; Alexander et al., 2012). While bushmeat contributes to food security (Rentsch and Damon, 2013; Schulte-Herbrügen et al., 2013), the benefits are unlikely to persist in the face of increasing demand and declining wildlife resources (Bennett, 2002). Unfettered hunting can harm human communities by restricting ecosystem services, wildlife-based industries, and sustainable yields of wild meat (Lindsey et al., 2013).

While most research into the ecological impacts of bushmeat hunting has focused on tropical forest ecosystems, bushmeat hunting

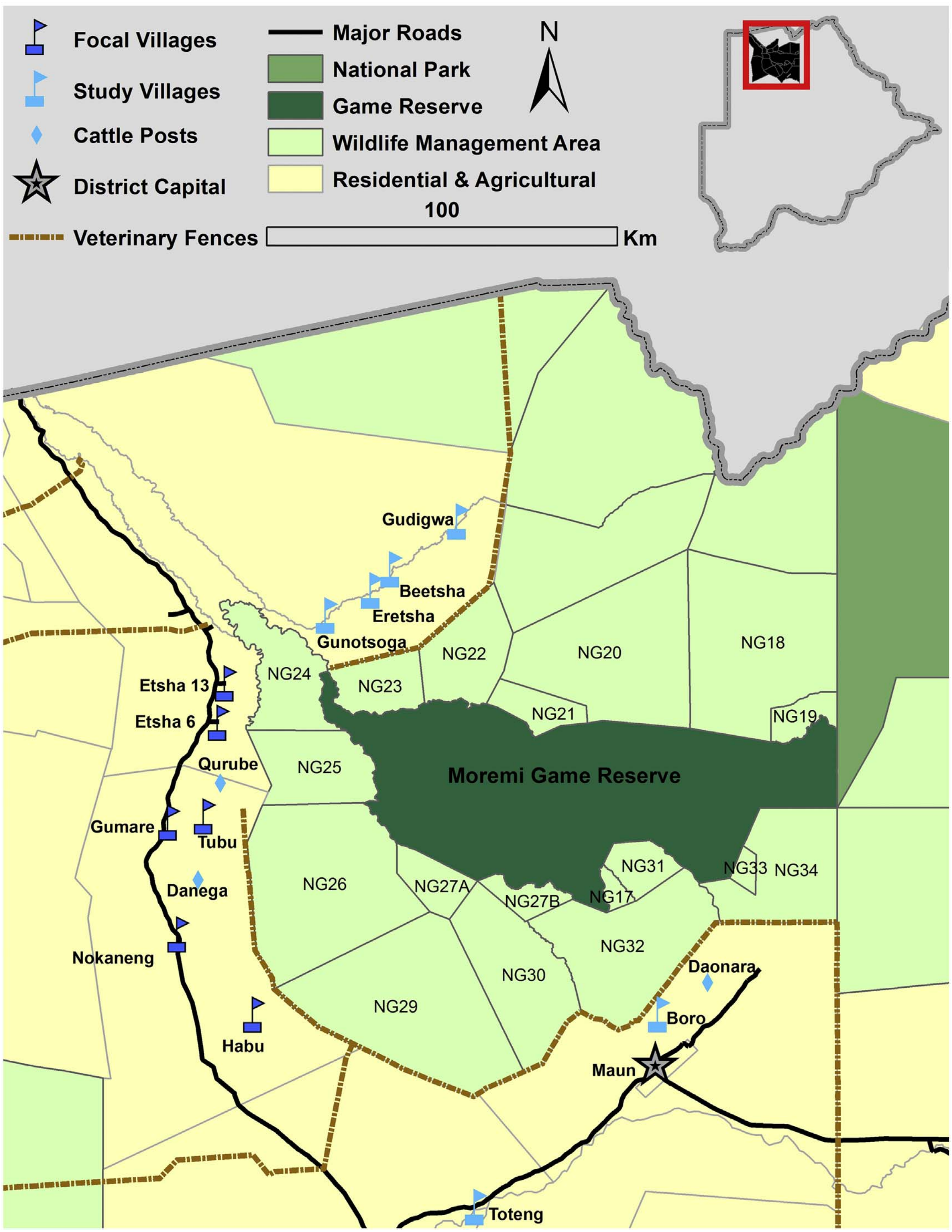

Fig. 1. Map of the Okavango Delta and study villages. In focal villages and noted cattle posts, research assistants worked intensively to identify and interview bushmeat hunters. In non-focal villages, research assistants interviewed hunters opportunistically.

in savannah ecosystems poses a unique set of socioecological challenges. Savannahs host rich vertebrate communities that are ecologically and economically valuable. Photographic tourism, which depends on intact wildlife communities, can be a social and economic boon (Snyman and Spenceley, 2012). Where the potential for wildlife-based tourism exists, illegal bushmeat hunting is an inefficient use of wildlife resources (Lindsey et al., 2015). Too frequently, however, the financial benefits of wildlife-based tourism do not reach impoverished communities near or within protected areas (PAs; Mbaiwa, 2005a; Wong, 2013). Consequently, local households may not receive direct benefits from wildlife other than through hunting (Lindsey et al., 2013). Additionally, these same communities may endure most costs associated with wildlife, such as crop raiding, livestock depredation, and opportunity costs when land is gazetted (Adams et al., 2004; Snyman and Spenceley, 2012).

Although many African countries have laws regulating legal hunting of game species, illegal bushmeat hunting is pervasive and increasingly commercial (Brashares et al., 2004; Fa and Brown, 2009; Lindsey et al., 2013; Rentsch and Damon, 2013). Illegal hunting is a particular challenge to wildlife conservation because of its pervasive, unregulated, and secretive nature (Knapp et al., 2010). In some African countries, perceptions that hunting is a traditional subsistence activity with limited effects on wildlife undermine enforcement of hunting laws (Lindsey et al., 2013). Improved understanding on the nature and impacts of illegal bushmeat hunting is essential to guide interventions addressing the issue.

We investigated illegal bushmeat hunting in the Okavango Delta in northern Botswana (hereafter “the delta”), in order to establish its scale and ecological impacts and to inform conservation interventions. Although Botswana is not traditionally associated with high levels of poaching, we found that illegal hunting occurs on a significant scale in the delta, poses a risk to wildlife populations, results in direct competition with large predators, and may ultimately impair the local tourism industry.

2. Methods

2.1. Study area

The delta is a depression in the Kalahari basin that encompasses a mosaic of permanently dry savannah and Mopane woodland, seasonally flooded plains, and permanent swamp (McNutt, 1996). In 2014, UNESCO designated 20,236 km^2 of the Okavango as a world heritage site with the 4610 km^2 Moremi Game Reserve (MGR) at its core (Mbaiwa, 2005b). Surrounding the game reserve are 18 Wildlife Management Areas (WMAs) the government leases to private entities or to community-based trusts under the Community-Based Natural Resource Management (CBNRM) program. Most of these WMAs are exclusively for wildlife-based uses and all of them prohibit livestock. The 18 WMAs and MGR span 18,195 km^2 (Fig. 1).

We conducted interviews in 12 villages located within mixed-use land concessions adjacent to WMAs (hereafter designated “residential concessions”). Residential concessions include residential communities, small-scale crop and livestock farming, and some ecotourism enterprises. The residential communities consist of formal villages with civic infrastructure and informal cattle posts – single households or small settlements - located outside the village proper where farmers tend remote crop fields and free-ranging herds of livestock. Veterinary control fences separate residential concessions from WMAs to prevent livestock-wildlife interactions. The few villages inside WMAs participating in Botswana's CBNRM program were excluded from this study.

All study villages were located within 35 km of WMAs, a distance consistent with previous reports of how far bushmeat hunters travel (Loibooki et al., 2002). We included 39% of villages in the study area as focal villages (Statistics Botswana, 2014) to ensure that selected villages were representative of the study area as a whole. Study villages varied geographically, ethnically, and economically. Six villages were part of ongoing CBNRM projects and six were not. Study village economies varied from mainly pastoral to predominantly crop farming. Communities ranged in size from 35 residents to ~9000 (Statistics Botswana, 2014).

Due to the size of the delta and the challenges inherent in convincing people to acknowledge and discuss illegal activities, we concentrated efforts to identify and interview hunters in six focal villages adjacent to four WMAs in the western delta. We chose this focal area because we consider those WMAs representative of the delta and because of documented illegal hunting there (911 Anti-poaching Operations Centre, unpublished data). The focal WMAs encompassed a variety of habitat types from permanent swamp to dry woodland. They exhibit management scenarios ranging from minimal management with minimal tourism (NG 24) to intensive tourism and private anti-poaching operations (NG 26). One concession, NG 24, is leased to a community trust under the CBNRM program, while the other three are leased to private companies. We supplemented western-delta hunter interviews with opportunistic interviews with hunters in the northern and southern portions of the delta.

Botswana is widely credited for strong commitments to wildlife conservation (Lindsey, 2010) and anti-poaching (Henk, 2005; Hoon, 2013). It has sought to engage local communities through CBNRM initiatives (Pienaar et al., 2013). The safari industry predominantly follows a high-value low-impact model of tourism designed to minimize its environmental footprint (Magole and Magole, 2011). With a sparse human population and large PAs, northern Botswana may appear relatively insulated against the threat of bushmeat hunting. However, in 2014, the government curbed hunting on public lands due to concerns that wildlife populations were in decline. Some experts cited illegal bushmeat hunting as a potential contributing factor (Rogan et al., 2015). Recent wildlife surveys found decreasing populations across northern Botswana in some herbivore species (Chase, 2011; DWNP, 2013). However, imprecision restricts these surveys' power to identify population trends conclusively for most species. Ascertaining the extent of illegal hunting and its contribution to potential wildlife declines is a key pre-requisite to conserving the Okavango ecosystem and effectively managing the wildlife therein.

2.2. Interviews

With permission from the Ministry of Environment, Wildlife and Tourism [research permit EWT 8/36/4 xxvii (25)], we conducted questionnaire surveys and integrated available records on wildlife populations and hunting events to assess the scale and impacts of bushmeat hunting in the delta. Participation in interviews was voluntary and anonymous.

We hired local citizen interviewers based on their familiarity with study villages, language skills, knowledge of the bushmeat industry, and prior interviewing experience. They conducted interviews from August 2014–March 2015 in one of five local languages, depending on respondent preference. Interviews consisted of semi-structured questionnaires for hunters and heads of households. Questionnaires, adapted from Lindsey et al. (Lindsey et al., 2011b), included questions on households' social and economic characteristics, consumption patterns, perceptions of wildlife, and, in the case of self-identified bushmeat hunters, on hunting practices and bushmeat harvests (see Supplementary Materials 8.1–8.2).

We sampled the heads of households at randomly distributed points within each village. This sampling approach excluded households situated outside the village core as defined by manually drawn polygons. To compensate, we also conducted interviews with heads of households based at cattle posts. It was not possible to identify all cattle post locations and thus sample a truly random subset. We therefore used local knowledge to identify clusters of cattle posts in disparate geographic directions from the village centre and conducted 1–4 interviews at each cluster. The non-random cattle post component was critical to capturing the variation within delta communities.

Interviewers networked in study villages to build trust with community members and to identify hunters. We also identified hunters at households that acknowledged consuming bushmeat during household interviews, and through snowball sampling (Goodman, 1961). We attempted to interview every identified hunter in each village sampled. Hunters were informed that no information gathered would be used against them in any way and that the surveys were anonymous.

2.3. Supporting data

We examined records of all court cases in Ngamiland related to wildlife crimes between 1 January 2009 and 31 December 2014. We acquired human population data from the 2011 census (Statistics Botswana, 2014) and aerial wildlife census data from a 2014 dry season (August – November) survey (Elephants Without Borders, EWB, unpublished data). We generated population estimates for the large carnivore guild (lions *Panthera leo*, spotted hyaenas *Crocuta crocuta*, leopards *Panthera pardus*, cheetahs *Acinonyx jubatus*, and African wild dogs *Lycaon pictus*) from density estimates derived from studies conducted in similar habitats elsewhere in the Okavango (Cozzi et al., 2013; Golabek et al., unpublished data).

2.4. Analysis

We conducted all statistical analyses using R version 3.2.2 (R Core Development Team, 2015) and spatial analyses in ArcGIS 10.2 (ESRI, 2013). For data that were non-normally distributed, we used non-parametric simulations to estimate 95% confidence intervals by resampling with replacement 10,000 times.

2.5. Common hunting practices

Hunters reported up to three species they most target during hunts. We categorized species according to size, with species > 20 kg classified as large and < 20 kg classified as small (Coe et al., 1976). We then characterized hunters as targeting primarily small, large, or mixed-size species and compared the distribution of animal size classes relative to hunting methods to an expected even distribution of size classes using a Chi-Square goodness-of-fit test.

2.6. Estimating the number of illegal hunters

Due to the secretive nature of illegal hunting, estimates based on interview surveys are prone to underreporting (Knapp et al., 2010). Combining interview data with arrest records can validate and improve estimates of illegal hunting prevalence (Knapp et al., 2010). We therefore used three complimentary methods to estimate the total number of bushmeat hunters in the delta:

2.6.1. Random sample

Hunting intensity varies between small villages and larger population centres (Nielsen, 2006). We therefore classified villages as small (< 2000 residents) or large (> 2000), based on 2011 census data. We estimated the number of households in each village using the average number of people per household reported in the surveys. Asymptotic Gaussian approximation produced 95% confidence intervals for the proportion of households involved in hunting in small and large villages. We obtained an estimate (and a minimum and maximum) by summing the results for small and large villages. We estimated on average 1.5 hunters per hunting household, based on evidence from surveys (including intra-family sharing and generational transfer of hunting skills and weapons within some households) (Brown and Marks, 2007; see Supplementary Materials 8.3–8.4).

2.6.2. Conviction rates

We recorded the total number of Ngamiland residents convicted of wildlife crimes in or around the delta as described in magistrate court records of cases that opened and closed from 2009 to 2014. Using the sample of interviewed hunters, who reported whether they had convictions for wildlife-related crimes, we used non-parametric resampling to estimate with 95% confidence the minimum number of hunters necessary to result in the observed number of convictions. Due to low conviction rates among interviewed hunters, a maximum estimate was unobtainable (i.e., the upper bound is infinite).

2.6.3. Integrated method

To address the propensity for random samples to underestimate illegal activity (Knapp et al., 2010), we generated a “revised” estimate by integrating three additional sources of information into the estimates of hunting rates within small and large villages. We incorporated results from interviews conducted at cattle posts, the proportion of households reported by hunters in focus groups, and the number hunters interviewed in study villages. The resulting revised estimate was consistent with other estimates (see Supplementary Materials 8.3–8.4) and therefore was used as a ‘best estimate’ in subsequent analyses.

2.7. Bushmeat harvest

We defined each individual hunter's offtake as the cumulative weight of all animals he reported killing in the previous twelve months divided by the number of hunters in his typical hunting party. We used non-parametric resampling to estimate with 95% confidence the true mean offtake per hunter. We also estimated rates of commercial hunting, which we defined as the proportion of interviewed hunters who reported exchanging bushmeat for cash.

We modelled biomass consumption from bushmeat hunting and the large carnivore guild in relation to available biomass from medium to large herbivores (excluding elephants) and herbivore species' intrinsic growth rates. A species' intrinsic growth rate is a life-history trait that characterizes the maximum potential growth rate of a population given stable age demographics (Tanner, 1975). To capture spatial variation across the study area, we divided the area into four sections delineated by aerial transect routes (Fig. 2) conducted across 1–2 concessions. We estimated the intrinsic growth rate of biomass (φ) in the herbivore

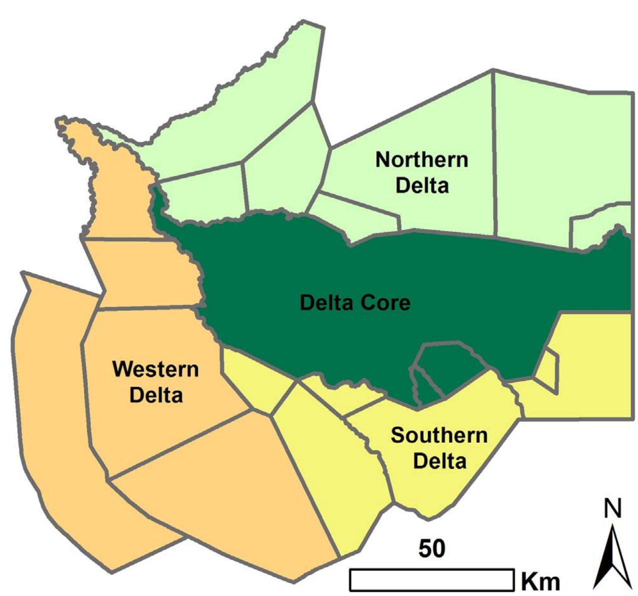

Fig. 2. Okavango Delta sub-regions for analysing the effects of illegal bushmeat hunting on herbivore population dynamics. Transect routes determined regional boundaries as some transects covered more than one WMA. The Delta Core comprises the Moremi Game Reserve and two small contiguous WMAs.

community (S) in a region (r) using Eq. 1 where P_{sr} represents the estimated population of herbivore species s in region r from the 2014 EWB aerial survey, $M_{s.}$ represents body mass of species s (from Coe et al., 1976). We assumed an intrinsic growth rate for herbivore species that breed annually and produce a single young per year of 1.2 per year (Owen-Smith, 2015). Warthog produce more than a single offspring per year and therefore intrinsic growth rate was estimated using the expected relationship between ungulate body mass and intrinsic growth rates, giving an intrinsic growth rate of 1.27 (Bothma, 2002).

Total estimated annual biomass offtake from poaching (β) in a region (r) is given by Eq. 2 where H_r is the estimated number of hunters in region r, and $\overline{k_s}$ and $\overline{w_s}$ represent the average number of individuals from species *s* that hunters kill and wound respectively. We derived H_r from the revised estimate of hunters apportioned to each region based on the population of adjacent villages. Anti-poaching reports from one focal concession (NG 26) indicate that un-butchered carcasses with gunshot wounds are common (Bushcraft APU, unpublished data). For the purposes of this model, we assumed half of all animals hunters report wounding die. We estimated annual biomass consumption by the large carnivore guild (β_{Cr}) using Eq. 3 where β_{dc} is the average daily adult consumption for carnivore species c (Mills and Biggs, 1993), P_{rc} is the estimated population of carnivore species c in region r, and 0.9 is the estimated adult proportion of carnivore populations. We reduced annual spotted hyena consumption by 50% to account for scavenging (including mortalities resulting from gunshot wounds).

We assumed that hunting levels in the delta “core” (see Fig. 2) are insignificant, based on testimony from illegal hunters and observations from land managers. We tested the effects of hunting in 1) the western delta (where data are most comprehensive), 2) the three peripheral regions collectively, and 3) the entire delta.

$$\varphi_r = \frac{\sum_s^S (P_{sr} + P_{sr} \times 1.2) \times M_s - \sum_s^S P_{sr} \times M_s}{\sum_s^S P_{sr} \times M_s} \tag{1}$$

$$\beta_r = H_r \sum_s^S M_s \left(\overline{k_s} + \frac{1}{2}\overline{w_s}\right) \tag{2}$$

$$\beta_{Cr} \sum_c^C \beta_{dc} \times 365 \times P_{rc} \times 0.9 \tag{3}$$

Thus, we summarize the impact of bushmeat hunting is reflected in the difference, with and without hunting, between total biomass consumption and the intrinsic growth of herbivore biomass.

We applied a sensitivity analysis to the herbivore biomass model to determine the relative importance of variables and to test the robustness of underlying assumptions. We varied predator (individual predator population size), hunter (poacher numbers, average offtake per hunter) and prey population (starting size and intrinsic growth rate) characteristics simultaneously and ran 1000 Monte Carlo simulations. For all count data we drew values from a random uniform distribution ± 10% of observed values and for rate variables we drew random variables from a random uniform distribution ± 0.1. To assess the relative importance of each variable we estimated the beta coefficient from linear models between the resulting change in biomass consumption (growth − offtake) and the spread of each variable's input values as drawn from the uniform distribution.

2.8. Edge effects from hunting

We designated areas < 15 km from a residential concession as edge habitat and areas > 15 km as interior habitat based on travel distances reported by illegal hunters and WMA managers. We tested the hypothesis that commonly-hunted species will be less abundant near the edge where they are susceptible to hunting (Lindsey et al., 2013) than in the interior (distinguished here from the “core” area referred to previously in Section 2.7) using transects of a 2014 dry-season aerial census (EWB

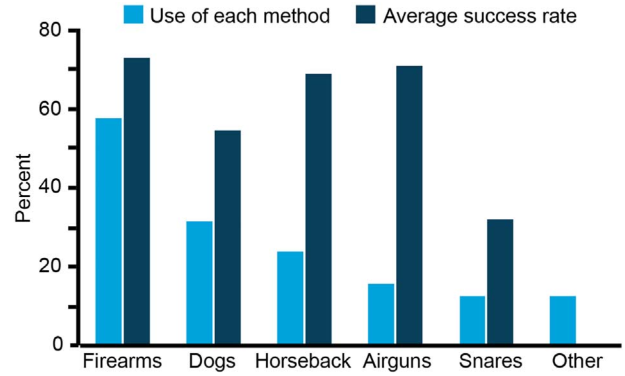

Fig. 3. Frequency of use and effectiveness of bushmeat hunting methods as reported by 91 bushmeat hunters.

2014 aerial survey).

Using transect segments ≥ 10 km we calculated encounters/km for each species and used the two-sample Kolmogorov-Smirnov to test for differences. To control for differences in habitat between the edge and interior, we compared the habitat composition using a habitat classification of three habitat classes (swamp, grassland, and woodland) from 30 m Landsat 5 Thematic Mapper imagery (N.A.S.A. Landsat Program, 1994; K. Collins, unpublished data).

3. Results

Ninety-one self-identified bushmeat hunters and 431 heads of households (367 randomly-sampled households and 64 selected households in cattle posts) participated in interviews. Non-response rates were below 3%, indicating a low risk of response bias (Groves, 2006).

3.1. Common hunting practices

Firearms were the most common hunting weapon, with 58% of interviewed hunters reporting their use (Fig. 3). Interviews also revealed that many hunters (24%) run animals down on horseback and kill them with axes or clubs (thus avoiding the sound of gunshots). Thirteen percent of interviewed hunters acknowledged using snares and none reported using gin traps. The choice of hunting weapon depended on the size of prey that hunters targeted (n = 139 as some hunters used multiple methods, $\chi^2 = 76.7$, df = 12, $p < 0.001$). Hunters using firearms or hunting from horseback primarily targeted large game, while those using dogs targeted small mammals. Hunters used airguns exclusively for hunting game birds. Interviews revealed that most hunting occurs outside of protected areas between the veterinary fences that encompass the delta WMAs and the roads that encircle the delta 10–30 km from the WMA boundaries. Twenty-one percent of hunters, however, acknowledged hunting inside protected areas.

Delta hunters frequently kill, and occasionally target, small carnivores. Twenty-seven hunters reported killing small carnivores, including black-backed jackals *Canis mesomelas*, civets *Civettictis civetta*, and African wild cats *Felis silvestris*, but only two reported targeting them. Among medium and large prey species, hunters reported killing impala *Aepyceros melampus* most often, followed by kudu *Tragelaphus strepsiceros* and buffalo *Syncerus caffer* (Fig. 4). Our data contrast with official reports of hunting incidents, which identified buffalo and giraffe *Giraffa camelopardalis* as the most commonly-hunted bushmeat species. One private anti-poaching unit accounted for most records of other bushmeat species. Many of the small, most commonly hunted species did not appear in any records of illegal hunting incidents.

3.2. Number of illegal bushmeat hunters

Among randomly-sampled heads-of-households, 13.7% of respon-

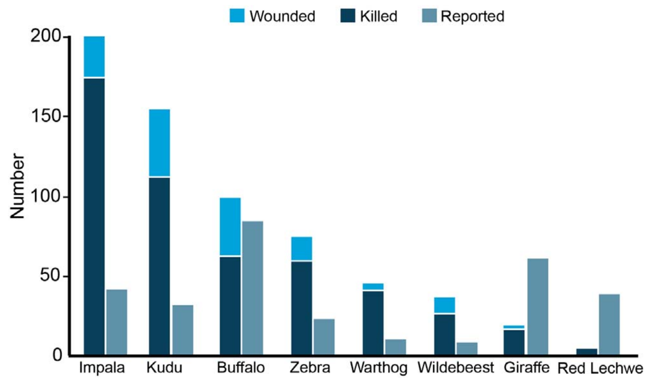

Fig. 4. Reported hunting of selected large mammals. Killed and wounded represent the number of individuals that bushmeat hunters (n = 90) reported hunting in the twelve months prior to the interview. Official records represent unique records from January 2009 – March 2015 sourced from court cases, police and DWNP reports, and private records.

dents in small villages (n = 248; village range: 3–50%) and 7.6% in large villages (n = 119; village range: 0–13%) reported that household members hunt for bushmeat (Table 1). Based on these proportions, the delta hosts approximately 1239 illegal hunters (95% CI: 576–1902; see Supplementary Materials 8.3–8.4). The 95th percentile bootstrapped conviction rate for illegal hunters suggested that at least 1523 hunters operate in the delta. The revised method data produced an estimate of 1787 hunters in the delta, 42% above the random-sample estimate but within the 95% confidence interval.

3.3. Bushmeat harvest

Among hunters who reported their bushmeat harvest for the previous 12 months (n = 90), the average harvest was 320 kg, (95% CI: 230–422 kg, range: 0.5–2625 kg), which corresponds to 172 kg dressed weight (median 88 kg). On average, hunting parties consisted of 3.3 people. Three hunters reported harvesting at least 1800 kg per member of their respective hunting parties. These three individuals accounted for 22% of all meat that interviewed hunters reported harvesting. The top 20% of hunters (n = 18) harvested 68% of the bushmeat. Buffalo accounted for 30% of all bushmeat production, followed by kudu (17%) and giraffe (12%). Impala, the most commonly hunted ungulate, accounted for 9% of all bushmeat.

3.4. Impacts of bushmeat hunting on large herbivore populations

The estimated harvest of individual species by bushmeat hunters ranged from ~2–20% of populations (Table 2). Kudu suffered the highest proportional offtake and was the only species harvested at rates approximately equivalent to its intrinsic growth rate (not considering other sources of mortality).

Large carnivores consume an estimated 19.7% of herbivore biomass in the delta annually, just under the intrinsic biomass growth rate of 20% (Table 3). This proportion varied by region, however, ranging from 14.4% in the delta core to 23% on the periphery. Offtake from bushmeat hunting (mean: ~348 kg/hunter/year) was 4.7% of herbivore biomass in the western delta, and 3.7% in the three peripheral regions. Consequently, total consumption exceeded the intrinsic growth rate in both the western delta and the periphery. Across the delta as a whole, humans and carnivores consumed 2.0% more biomass than herbivore populations can produce annually. Hunters removed more biomass from the western delta than all carnivores except for lions and spotted hyaenas, and more than cheetahs and wild dogs in the delta as a whole.

Over 1000 Monte Carlo simulations, 98.9% of runs resulted in a decline in herbivore biomass (i.e. total offtake exceeded intrinsic growth) at the ecosystem scale, with 95% of runs producing a decline of 0.5% or greater. Herbivore populations and intrinsic growth rate exhibited the strongest effects on the model outcomes, with beta coefficients of 0.54 and 0.53, respectively (Fig. 5). Predators ($\beta = -0.31$) exhibited an impact nearly four times greater than bushmeat hunting ($\beta = -0.08$). Average offtake per hunter ($\beta = -0.077$) was half again as important as the number of hunters ($\beta = -0.051$). When considering only the western delta, results were similar, but predation had an effect only 60% greater than bushmeat hunting, and the number of hunters had an effect broadly equivalent to average offtake.

3.5. Edge effects from hunting

Five species exhibited higher average relative abundance in the interior than in the edge, and five species had higher average relative abundance in the edge (see Supplementary Materials 8.5). Impala was the only species that was < 75% as abundant in the edge as in the interior, however the difference was not significant (Kolmogorov-Smirnov Test, p = 0.11).

4. Discussion

4.1. Common hunting practices

Illegal bushmeat hunting is common and widespread in the delta. The prevalence of firearms is evidence that bushmeat hunting is lucrative (Damania et al., 2005). The practice of running animals down on horseback, which is a recent development (M.A.P. Ives, personal communication, July 2014), mirrors findings in Tanzania where poachers employ a similar tactic with motorbikes (Kiffner et al., 2014). Although firearm use and conviction rates suggest that the risk of detection is low, the rise of hunting on horseback without firearms suggests that detection is a concern for some hunters, particularly those hunting inside protected areas. We hypothesize that secretive methods will become more prolific if law enforcement efforts intensify.

We would expect to see the hunters employ the most effective methods most frequently. This was not always the case. Airguns and horses were more effective than hunting with dogs but employed less often. The size of targeted species explains some of this difference, with airguns used almost exclusively to hunt game birds and horses used only to hunt large game. The skill necessary to hunt from horseback, and access to horses, may also limit its use. In contrast, dogs are effective across a wide range of small and medium-sized species, and

Table 1
Parameters for estimating with 95% confidence the number of households that participate in bushmeat hunting around the Okavango Delta based on the random sample of heads-of-households.

	Sampled households that hunt	Total sample size	Percent of households that engaged in hunting	Total population	Number of households	Estimated number of hunter households	Lower bound	Upper bound
Small villages (< 2000)	34	248	13.7%	15,323	2554	350	240	460
Large villages (≥ 2000)	9	119	7.6%	37,559	6260	476	144	808

Table 2
Estimated annual offtake of selected species from bushmeat hunting in the Okavango Delta, and comparison to estimates of population size. Zebra and red lechwe are excluded due to geographic biases in the sample of interviewed hunters relative to those species' predominant habitat. *Based on revised estimate of 1787 hunters, includes average killed and 0.5 * average wounded. #EWB 2014 Aerial Survey (EWB, unpublished data). ϴ Based on calculations adopted from Bothma (2002). †Partial count.

Selected species	Estimated annual offtake from hunting*	Estimated population#	Hunting offtake as a proportion of total estimated population	Estimated bushmeat harvest (kg dressed weight)
African Buffalo (*Syncerus caffer*)	499	15,893†	0.03	95,783
Blue Wildebeest (*Connochaetes taurinus*)	170	2108	0.08	14,515
Giraffe (*Giraffa camelopardalis*)	99	3823	0.03	32,669
Greater Kudu (*Tragelaphus strepsiceros*)	838	4138	0.20	54,581
Hippopotamus (*Hippopotamus amphibious*)	25	6334	0.02	13,885
Impala (*Aepyceros melampus*)	1363	65,044	0.02	30,075
Sable Antelope (*Hippotragus niger*)	71	792	0.09	5437
Sitatunga (*Tragelaphus spekii*)	16	478	0.03	375
Warthog (*Phacochoerus africanus*)	243	3710	0.08	3677
Waterbuck (*Kobus ellipsiprymnus*)	20	385	0.05	2255

Table 3
Estimated consumption of medium–large herbivores by large carnivores and bushmeat hunters, and the effects of consumption of herbivore biomass in the Okavango Delta, Botswana. The periphery refers to the west, north, and south regions collectively.

	West	Periphery	Core	Total
Biomass available (kg)	6,899,593	16,816,780	10,321,878	27,138,658
Hunter offtake (kg)	324,398	622,343	0	622,343
Lion consumption (kg)	527,768	1,411,827	571,590	1,983,417
Leopard consumption (kg)	303,534	900,484	329,551	1,230,035
Cheetah consumption (kg)	22,765	68,295	24,835	93,130
Wild dog consumption (kg)	82,782	244,897	89,681	334,577
Hyaena consumption (kg)	429,415	1,249,548	465,616	1,715,164
Total consumption (kg)	1,651,314	4,497,395	1,481,272	5,978,667
Total consumption (%)	23.9%	26.7%	14.4%	22.0%
Bushmeat consumption (%)	4.7%	3.7%	0%	2.3%
Biomass growth (%)	20.0%	20.1%	20.0%	20.0%
Change (%)	− 3.9%	− 6.7%	5.7%	− 2.0%
Outcome	Decline	Decline	Growth	Decline
Consumption (No hunting, %)	19.8%	23.0%	14.4%	19.7%

may be practical for the most opportunistic hunters.

The frequent killing of small carnivores is an unusual phenomenon in bushmeat hunting. The resilience of jackals, and potentially other mesocarnivores, to persecution may result in sustained populations close to villages despite intense hunting pressure (Minnie et al., 2016). In other respects, species selection mirrored Martin et al.'s (2013) findings, with hunters primarily targeting large common species but actually killing higher proportions of rare species. Kudu, wildebeest, and zebra epitomize this trend, as they are common on the edges of the delta closest to human settlements, but less common at the ecosystem scale.

Only a fifth of hunters reported hunting inside protected areas. The abundance of wildlife outside protected areas appears to be the main reason, rather than risk concerns (Rogan et al., 2015). We expect that hunting inside protected areas will increase if wildlife declines outside PAs.

The discrepancy between the species reported killed in official records and the species that hunters reported killing most frequently suggests a systematic failure to detect illegal hunting of all but the largest species. Detection bias likely accounts for the higher prevalence of giraffe and buffalo in official reports because hunters are generally not able to remove the carcasses of those species. Localized reports from Bushcraft APU (unpublished data), however, show that effective enforcement allows for detection of the hunting of smaller animals even when hunters remove entire carcasses.

4.2. Numbers of illegal bushmeat hunters

The multi-method approach suggests that there are 1500–2000 operating in the delta. Both the revised estimate and the conviction rate estimate suggest that the random sample was prone to undercounting as expected (Knapp et al., 2010). Therefore, we consider a reasonable possibility that the true number of hunters exceeds the random sample's 95% confidence limit of 1902 hunters. The best estimate of 1787 hunters represents 5% of men aged 15–64 in Ngamiland (Statistics Botswana, 2014). Observed hunting rates were consistent with those reported across Tanzania (Ceppi and Nielsen, 2014), and lower than reported in a localized study of Tanzanian communities close to a national park (Kiffner et al., 2015). In rural communities with abundant wildlife, this hunting rate is thus lower than we might expect, particularly in a society in which hunting was traditionally ubiquitous and where firearms are common. Bushmeat hunting is nevertheless sufficiently pervasive and intensive to be a major issue for wildlife management in Ngamiland. Our estimate provides a snapshot of current hunting intensity and ongoing monitoring is critical to track the extent of illegal hunting and to assess the effectiveness of interventions.

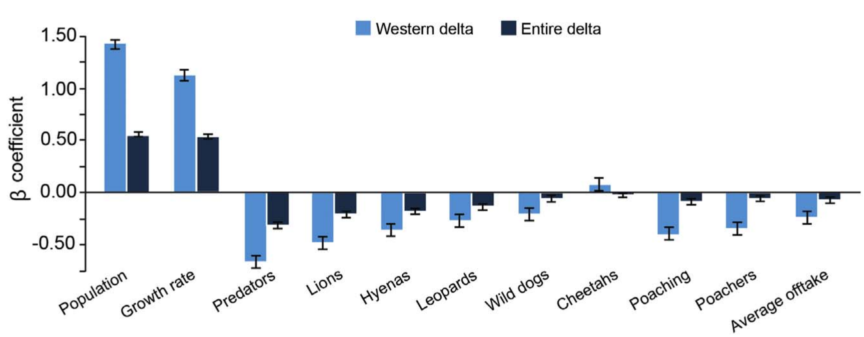

Fig. 5. Beta coefficients of variables in the herbivore biomass model for the entire delta and the western region based on 1000 simulations in which variables fluctuated ± 10% following a Gaussian distribution.

4.3. Bushmeat harvest

While most hunters reported hunting exclusively for home consumption, several hundred also sell meat. The large quantities of bushmeat (~2000 kg) reported by some hunters suggests the existence of an organised commercial element to the industry, with capacity to harvest, transport and dispose of significant volumes. Even less intensive hunters are harvesting sufficient bushmeat to meet a considerable portion of household demand. The median dressed weight bushmeat harvest (88 kg) is equivalent to 40% of an average 6-person Botswanan household's annual meat consumption (FAO, 2011). For non-commercial hunters (~70% of hunters), bushmeat represents a nearly costless substitute for livestock meat, and thus allows for significant savings. Demand for bushmeat among consumers who purchase the product is driven by various factors, including price, availability and taste preferences (Rogan et al., 2015).

4.4. Ecological impacts

With the exception of kudu, harvests from bushmeat hunting were well below estimated intrinsic growth rates. However, the delta supports important populations of apex predators that depend on many of these same species for prey. Bushmeat hunters compete directly with carnivores for prey and as a result reduce the carrying capacity of the area for those species (Henschel et al., 2011). We acknowledge that our biomass offtake model relies on coarsely estimated inputs, yielding imprecise estimates of the relationship between biomass offtake and growth. The sensitivity analysis, however, illustrates that even accounting for potential error in inputs, consumption of predators and bushmeat hunters almost certainly exceeds sustainable levels. Illegal bushmeat hunting thus poses a real threat to the delta's wildlife.

These effects are consistent with outcomes observed in a wetland-woodland ecosystem of Rukwa-Katavi, Tanzania, where comparable levels of offtake, including disproportionate hunting of uncommon species, coincided with steep declines in wildlife populations (Martin and Caro, 2013; Martin et al., 2013). Our findings help explain observed declines in some species of herbivores, particularly intensively hunted species such as kudu, giraffe, and wildebeest (Chase, 2011; DWNP, 2013).

The sensitivity analysis also revealed the importance of hunting intensity (i.e., offtake per hunter) relative to the number of hunters. This relationship suggests that delta wildlife populations are particularly vulnerable to the commercialization of bushmeat hunting. Demand for bushmeat in Ngamiland is likely to increase with human population growth, which, in the absence of increased law enforcement, could lead to further commercialization of the bushmeat trade. Numerous additional factors, including climate change and reduction of the delta floodplains through decreased flood volumes, will further compromise the present-day productivity and herbivore carrying capacity of the Okavango ecosystem (Murray-Hudson et al., 2006). These trends suggest that the relative impacts of bushmeat hunting quickly will become more severe.

In addition, prey depletion caused by bushmeat hunting may increase human-carnivore conflict (Valeix et al., 2012; Khorozyan et al., 2015), and retaliatory killings of wild carnivores. These factors may explain the delta's declining lion population over the previous decade (Fuller and Sievert, 2001; Winterbach et al., 2012; Bauer et al., 2015).

4.5. Edge effects from hunting

We did not find evidence supporting our hypothesis that bushmeat hunting depresses wildlife populations on the delta's periphery compared to its un-hunted interior. Our findings may reflect variation in habitat suitability or seasonal wildlife movements (Bartlam-Brooks et al., 2013; Bennitt et al., 2014), but they may also reflect consistent movement of herbivores from a population source in the core to a population sink in the edge. Because the delta core is highly productive and experiences minimal bushmeat hunting, local movement could theoretically compensate for the offtake of species in peripheral WMAs. Trends from other savannah ecosystems suggest that in actuality locally concentrated bushmeat hunting can negatively affect wildlife populations across an entire ecosystem rather than conferring localized impacts (Kiffner et al., 2013; Midlane, 2013).

4.6. Economic and social impacts

Excessive bushmeat harvests have potential to confer negative economic impacts on both a local and national level. The Okavango's globally renowned wildlife is critical to Botswana's high-value tourism and is the key attraction for foreign tourists (Mladenov et al., 2007). Wildlife based tourism is a driver of economic growth and job creation in Botswana, contributing 70,000 jobs and nearly 10% of GDP (World Travel and Tourism Council, 2015). Illegal hunting for bushmeat threatens the growth of this important industry through its potential to impart population declines of herbivores and reduce the carrying capacity for large predators, on which the tourism industry depends (Di Minin et al., 2013).

4.7. Implications for conservation

We recommend a holistic approach to addressing illegal hunting in the Okavango, including effective law enforcement on the delta's periphery (Hilborn et al., 2006) and the development of wildlife tourism ventures in the Okavango's peripheral areas that generate employment for members of local communities. Interventions should focus on increasing incentives to conserve wildlife while simultaneously increasing the risks of hunting illegally (Biggs et al., 2017; Knapp, 2012; Rogan et al., 2015). Success may depend on changes to legal frameworks that empower communities to benefit from wildlife significantly, in ways other than through illegal hunting (Lindsey et al., 2015). Wildlife managers must seek ways to engage local communities in wildlife tourism industries more effectively through partnerships and employment. Finally, policies are required that promote legal wildlife ranching and the distribution of game meat so that legal harvests can meet demand for the product. Communities in the lands adjacent to the delta need opportunities to participate in such land uses.

4.8. Conclusions

Our study underscores the threat illegal bushmeat hunting poses to wildlife in African savannahs and to the prospects of wildlife-based tourism industries. Even in Botswana, a middle-income country with a relatively well-resourced wildlife authority and low human population density, illegal hunting constitutes a serious threat to wildlife populations. The bushmeat trade is a complex problem that links food security, development, culture, and conservation, and which demands multifaceted interventions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.04.020.

References

Abernethy, K.A., Coad, L., Taylor, G., Lee, M.E., Maisels, F., 2013. Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. Philos. Trans. R. Soc. B 368, 20120303.
Adams, W.M., Aveling, R., Brockington, D., Dickson, B., Elliott, J., Mutton, J., Dilys, R., Vira, B., Wolmer, W., 2004. Biodiversity conservation and the eradication of poverty. Science 306, 1146–1149.
Alexander, K.A., Blackburn, J.K., Vandewalle, M.E., Pesapane, R., Baipoledi, E.K., Elzer, P.H., 2012. Buffalo, bush meat, and the zoonotic threat of brucellosis in Botswana. PLoS One 7, e32842.
Bartlam-Brooks, H.L.A., Beck, P.S.A., Bohrer, G., Harris, S., 2013. In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration. J. Geophys. Res. 118, 1427–1437.
Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T.B., Macdonald, D.W., Dloniak, S.M., Packer, C., 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. PNAS 112, 14894–14899.
Becker, M., McRobb, R., Watson, F., Droge, E., Kanyembo, B., Murdoch, J., Kakumbi, C., 2013. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. Biol. Conserv. 158, 26–36.
Bennett, E.L., 2002. Is there a link between wild meat and food security? Conserv. Biol. 16, 590–592.
Bennitt, E., Bonyongo, M.C., Harris, S., 2014. Habitat selection by African buffalo (*Syncerus caffer*) in response to landscape-level fluctuations in water availability on two temporal scales. PLoS One 9, e101346.
Biggs, D., Cooney, R., Roe, D., Dublin, H., Allan, J.R., Challender, D., Skinner, D., 2017. Developing a theory of change for a community-based response to illegal wildlife trade. Conserv. Biol. (31), 5–12.
Bothma, J.D.P. (Ed.), 2002. Game Ranch Management, fourth ed. Van Schalk, Pretoria, South Africa.
Brashares, J.S., Arcese, P., Sam, M.K., Coppolillo, P.B., Sinclair, A.R.E., Balmford, A., 2004. Bushmeat hunting, wildlife declines, and fish supply in West Africa. Science 306, 1180–1183.
Brown, T., Marks, S., 2007. In: Davies, G., Brown, D. (Eds.), Livelihoods, Hunting and the Game Meat Trade in Northern Zambia. Blackwell, Oxford, pp. 92–106.
Ceppi, S.L., Nielsen, M.R., 2014. A comparative study on bushmeat consumption patterns in ten tribes in Tanzania. In: Tropical Conservation Science. Vol. 7. pp. 272–287.
Chase, M., 2011. Dry Season Fixed-wing Aerial Survey of Elephants and Wildlife in Northern Botswana. Elephants Without Borders, Kasane, Botswana.
Coe, M.J., Cumming, D.H.M., Phillipson, J., 1976. Biomass and production of large African herbivores in relation to rainfall and primary productivity. Oecologia 22, 341–354.
Core Development Team, R., 2015. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Cozzi, G., Broekhuis, F., McNutt, J.W., Schmid, B., 2013. Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation. Biodivers. Conserv. 22, 2937–2956.
Damania, R., Milner-Gulland, E.J., Crookes, D.J., 2005. A bioeconomic analysis of bushmeat hunting. Proc. R. Soc. B 272, 259–266.
Department of Wildlife and National Parks, 2013. Aerial Census of Animals in Northern Botswana: Dry Season 2013. Department of Wildlife and National Parks, Gaborone, Botswana.
Di Minin, E., Fraser, I., Slotow, R., MacMillan, D.C., 2013. Understanding heterogeneous preference of tourists for big game species: Implications for conservation and management. Anim. Conserv. 16, 249–258.
ESRI, 2013. ArcGIS desktop. In: Institute ESR, Editor, (Release 10.2 ed. Redlands, CA).
Fa, J.E., Brown, D., 2009. Impacts of hunting mammals in African tropical moist forests: a review and synthesis. Mammal Rev. 39, 231–264.
Food and Agriculture Organization of the United Nations, 2011. Food Supply – Livestock and Fish Primary Equivalent. (http://www.fao.org/faostat/en/#data/CL. Accessed November 2016).
Fuller, T.K., Sievert, P.R., 2001. Carnivore demography and the consequences of changes in prey availability. In: Gittleman, J.L., Funk, S.M., Macdonald, D.W., Wayne, R.K. (Eds.), Carnivore Conservation. Cambridge University Press, Cambridge, pp. 163–178.
Galetti, M., Dirzo, R., 2013. Ecological and evolutionary consequences of living in a defaunated world. Biol. Conserv. 163, 1–6.
Goodman, L.A., 1961. Snowball sampling. Ann. Math. Stat. 32, 148–170.
Groves, R.M., 2006. Nonresponse rates and nonresponse bias in household surveys. Public Opin. Q. 70, 646–675.
Harrison, R.D., Sreekar, R., Brodie, J.F., Brook, S., Luskin, M., O'Kelly, H., Rao, M., Scheffers, B., Velho, N., 2016. Impacts of hunting on tropical forests in Southeast Asia. Conserv. Biol. 30, 972–981. http://dx.doi.org/10.1111/cobi.12785.
Henk, D., 2005. The Botswana Defence Force and the war against poachers in southern Africa. In: Small Wars and Insurgencies. Vol. 16. pp. 170–191.
Henschel, P., Hunters, L.T.B., Coad, L., Abernethy, K.A., Mühlenberg, M., 2011. Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters. J. Zool. 285, 11–20.
Hilborn, R., Arcese, P., Borner, M., Hando, J., Hopcraft, G., Loibooki, M., Mduma, S., Sinclair, A.R.E., 2006. Effective enforcement in a conservation area. Science 314, 1266.
Holmern, T., Mkama, S., Muya, J., Røskaft, E., 2006. Intraspecific prey choice of bushmeat hunters outside the Serengeti National Park, Tanzania: a preliminary analysis. Afr. Zool. 41, 81–87.
Hoon, P., 2013. Militarizatio of African wildlife conservation? In: Embedding of Anti-poaching and the Hidden Role of the Botswana Defense Force. Social Science Research Network. http://ssrn.com/abstract=2247182.
Karesh, W.B., Noble, E., 2009. The bushmeat trade: increased opportunities for transmission of zoonotic disease. Mt Sinai J. Med. 76, 429–434.
Khorozyan, I., Ghoddousi, A., Soofi, M., Waltert, M., 2015. Big cats kill more livestock when prey reaches a minimum threshold. Biol. Conserv. 192, 268–275.
Kiffner, C., Stoner, C., Caro, T., 2013. Edge effects and large mammal distributions in a national park. Anim. Conserv. 16, 97–107.
Kiffner, C., Kioko, J., Kissui, B., Serota, M., White, C., Yager, P., 2014. Interspecific variation in large mammal responses to human observers along a conservation gradient with variable hunting pressure. Anim. Conserv. 17, 603–612.
Kiffner, C., Peters, L., Stroming, A., Kioko, J., 2015. Bushmeat consumption in the Tarangire-Manyara ecosystem, Tanzania. In: Tropical Conservation Science. Vol. 8. pp. 318–332.
Knapp, E.J., 2012. Why poaching pays: a summary of risks and benefits illegal hunters face in Western Serengeti, Tanzania. In: Tropical Conservation Science. Vol. 5. pp. 434–445.
Knapp, E.J., Rentsch, D., Schmitt, J., Lewis, C., Polasky, S., 2010. A tale of three villages: choosing an effective method for assessing hunting levels in western Serengeti, Tanzania. Oryx 44, 178–184.
Kock, R.A., Kock, M., Cleaveland, S., Thomson, G., 2009. Health and disease in wild rangelands. In: Du Toit, J.T., Kock, R.A., Deutsch, J.C. (Eds.), Wild Rangelands: Conserving Wildlife While Maintaining Livestock in Semi-Arid Ecosystems. John Wiley & Sons, Chichester, pp. 98–128.
Koerner, S.E., Poulsen, J.R., Blanchard, E., Okouyi, J., Clark, C.J., 2016. Vertebrate community composition and diversity declines along a defaunation gradient radiating from rural villages in Gabon. J. Appl. Ecol. http://dx.doi.org/10.1111/1365-2664.12798.
Lindsey, P.A., 2010. The future of wildlife-based land uses in Botswana. Current Conservation 3, 23–24.
Lindsey, P.A., Romañach, S.S., Tambling, C.J., Chartier, K., Groom, R., 2011a. Ecological and financial impacts of illegal bushmeat trade in Zimbabwe. Oryx 45, 96.
Lindsey, P.A., Romañach, S.S., Matema, S., Matema, C., Mupamhadzi, I., Muvengwi, J., 2011b. Dynamics and underlying causes of illegal bushmeat trade in Zimbabwe. Oryx 45, 84–95.
Lindsey, P.A., Balme, G., Becker, M., Begg, C., Bento, C., Bocchino, C., Dickman, A., Diggle, R.W., Eves, H., Henschel, P., Lewis, D., Marnewick, K., Mattheus, J., McNutt, J.W., McRogg, R., Midlane, N., Milanzi, J., Morley, R., Murphree, M., Opyene, V., Phadima, J., Purchase, G., Rentsch, D., Roche, C., Shaw, J., van der Westhuizen, H., Vliet, N.V., Zisadza-Gandiwa, P., 2013. The bushmeat trade in African savannas: Impacts, drivers, and possible solutions. Biol. Conserv. 160, 80–96.
Lindsey, P.A., Taylor, W.A., Nyirenda, V., Barnes, J., 2015. Bushmeat, Wildlife-based Economies, Food Security and Conservation. Food and Agriculture Organization of the United Nations, Harare, Zimbabwe.
Lindsey, P.A., Petracca, L., Funston, P.J., Bauer, H., Dickman, A., Everatt, K., Flyman, M., Henschel, P., Hinks, A., Kasiki, S., Loveridge, A., Macdonald, D.W., Mandisodza, R., Mgoola, W., Miller, S., Nazerali, S., Siege, L., Usieb, K., Hunter, L., 2017. The performance of African protected areas for lions and their prey, determinants of success and key conservation threats. Biol. Conserv. 209, 137–149.
Loibooki, M., Hofer, H., Campbell, K.L.I., East, M.L., 2002. Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: the importance of livestock ownership and alternative sources of protein and income. Environ. Conserv. 29, 391.
Magole, L.I., Magole, L., 2011. Revisiting Botswana's high-value, low-volume tourism. Tour. Anal. 16, 203–210.
Marealle, W.N., Fossøy, F., Holmern, T., Stokke, B.G., Røskaft, E., 2010. Does illegal hunting skew Sereneti wildlife sex ratios? Wildl. Biol. 16, 1–11.
Martin, A., Caro, T., 2013. Illegal hunting in the Katavi-Rukwa ecosystem. Afr. J. Ecol. 51, 172–175.
Martin, A., Caro, T., Kiffner, C., 2013. Prey preferences of bushmeat hunters in an East African savannah ecosystem. Eur. J. Wildl. Res. 59, 137–145.
Mbaiwa, J.E., 2005a. Enclave tourism and its socio-economic impacts in the Okavango Delta, Botswana. Tour. Manag. 26, 157–172.
Mbaiwa, J.E., 2005b. Wildlife resource utilization at Moremi Game Reserve and Khwai community area in the Okavango Delta, Botswana. J. Environ. Manag. 77, 144–156.
McNutt, J.W., 1996. Sex-biased dispersal in African wild dog, *Lycaon pictus*. Anim. Behav. 52, 1067–1077.
Mgawe, P., Borgerhoff Mulder, M., Caro, T., Martin, A., Kiffner, C., 2012. Factors affecting bushmeat consumption in the Katavi-rukwa ecosystem of Tanzania. In: Tropical Conservation Science. Vol. 5. pp. 446–462.
Midlane, N., 2013. The conservation status and dynamics of a protected African lion *Panthera leo* population in Kafue National Park, Zambia. In: A Ph.D. Dissertation, December 2013. University of Cape Town, South Africa.
Mills, M.G.L., Biggs, H.C., 1993. Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. Symp. Zool. Soc. Lond. 65, 253–268.

Minnie, L., Gaylard, A., Kerley, G.I.H., 2016. Compensatory life-history responses of a mesopredator may undermine carnivore management efforts. J. Appl. Ecol. 53, 379–387.

Mladenov, N., Gardner, J.R., Flores, N.E., Mbaiwa, J.E., Mmopelwa, G., Strzepek, K.M., 2007. The value of wildlife-viewing tourism as an incentive for conservation of biodiversity in the Okavango Delta, Botswana. Dev. South. Afr. 24, 409–423.

Murray-Hudson, M., Wolski, P., Ringrose, S., 2006. Scenarios of the impact of local and upstream changes in climate and water use on hydro-ecology in the Okavango Delta, Botswana. J. Hydrol. 331, 73–84.

N.A.S.A. Landsat Program. Landsat 5 TM, SLC-Off, U.S.G.S, Sioux Falls.

Nielsen, M.R., 2006. Importance, cause and effect of bushmeat hunting in the Udzungwa Mountains, Tanzania: Implications for community based wildlife management. Biol. Conserv. 128, 509–516.

Owen-Smith, N., 2015. Mechanisms of coexistence in diverse herbivore–carnivore assemblages: demographic, temporal and spatial heterogeneities affecting prey vulnerability. Oikos 124, 1417–1426.

Pienaar, E.F., Jarvis, L.S., Larson, D.M., 2013. Creating direct incentives for wildlife conservation in community-based natural resource management programmes in Botswana. J. Dev. Stud. 49, 315–333.

Rentsch, D., Damon, A., 2013. Prices, poaching, and protein alternatives: An analysis of bushmeat consumption around Serengeti National Park, Tanzania. Ecol. Econ. 91, 1–9.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I.H., Levi, T., Lindsey, P.A., Macdonald, D.W., Malhi, Y., Painter, L.E., Sandom, C.J., Terborgh, J., van Valkenburgh, B., 2015. Collapse of the world's largest herbivores. Sci. Adv. 1, e1400103.

Ripple, W.J., Abernethy, K., Betts, M.G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P.A., Macdonald, D.W., Machovina, B., Newsome, T.M., Peres, C.A., Wallach, A.D., Wolf, C., Young, H., 2016. Bushmeat hunting and extinction risk to the world's mammals. Royal Society Open Science 3, 160498.

Rogan, M.S., Lindsey, P.A., McNutt, J.W., 2015. Illegal Bushmeat Hunting in the Okavango Delta, Botswana: Drivers, Impacts and Potential Solutions. Food and Agriculture Organization of the United Nations, Harare, Zimbabwe.

Schulte-Herbrügen, B., Cowlishaw, G., Homewood, K., Rowcliffe, J.M., 2013. The importance of bushmeat in the livelihoods of West African cash-crop farmings living in a faunally-depleted landscape. PLoS One 8, e72807.

Setsaas, T.H., Holmern, T., Mwakalebe, G., Stokke, S., Røskaft, E., 2007. How does human exploitation affect impala populations in protected and partially protected areas? – a case study from the Serengeti Ecosystem, Tanzania. Biol. Conserv. 136, 563–570.

Snyman, S., Spenceley, A., 2012. Key sustainable tourism mechanisms for poverty reduction and local socioeconomic development in Africa. Africa Insight 42, 76–93.

Statistics Botswana, 2014. Population and Housing Census 2011 Analytical Report. Statistics Botswana, Gaborone, Botswana.

Tanner, J.T., 1975. The stability and the intrinsic growth rates of prey and predator populations. Ecology 56, 855–867.

Valeix, M., Hemson, G., Loveridge, A.J., Mills, G., Macdonald, D.W., 2012. Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. J. Appl. Ecol. 49, 73–81.

Winterbach, H.E.K., Winterbach, C.W., Somers, M.J., Hayward, M.W., 2012. Key factors and related principles in the conservation of large African carnivores. Mammal Rev. 43, 89–110.

Wong, S., 2013. Challenges to the elite exclusion-inclusion dichotomy – reconsidering elite capture in community-based natural resource management. South African Journal of International Affairs 20, 379–391.

World Travel & Tourism Council, 2015. Travel & Tourism: Economic Impact 2015 Botswana. World Travel & Tourism Council, London, United Kingdom.