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The bushmeat and food security nexus: A global account of the contributions, conundrums and ethical collisions

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ABSTRACT

Wild meat or 'bushmeat' has long served as a principal source of protein and a key contributor to the food security of millions of people across the developing world, most notably in Africa, Latin America and Asia. More recently, however, growing human populations, technological elaborations and the emergence of a booming commercial bushmeat trade have culminated in unprecedented harvest rates and the consequent decline of numerous wildlife populations. Most research efforts aimed at tackling this problem to date have been rooted in the biological disciplines, focused on quantifying the trade and measuring its level of destruction on wildlife and ecosystems. Comparatively little effort, on the other hand, has been expended on illuminating the role of bushmeat in human livelihoods and in providing alternative sources of food and income, as well as the infrastructure to make these feasible. This paper aims to shift the focus to the human dimension, emphasising the true contributions of bushmeat to food security, nutrition and well-being, while balancing this perspective by considering the far-reaching impacts of overexploitation. What emerges from this synthesis is that bushmeat management will ultimately depend on understanding and working with people, with any approaches focused too narrowly on biodiversity preservation running the risk of failure in the long term. If wildlife is to survive and be utilised in the future, there is undoubtedly a need to relax adherence to unswerving biocentric or anthropocentric convictions, to appreciate the necessity for certain trade-offs and to develop integrated and flexible approaches that reconcile the requirements of both the animals and the people.

1. Introduction

Although often poorly recognised, nature's goods and services constitute the ultimate foundation of human life and health. Apart from delivering basic provisioning services such as food, water and medicinal resources, natural ecosystems fulfil other crucial supporting, regulating and cultural functions (Díaz, Fargione, Chapin, & Tilman, 2006). Over the past 50 years, however, mankind has altered ecosystems and the biodiversity they contain more rapidly and extensively than at any other time in history. Transformation of the planet has subsidised considerable net gains in human well-being and economic development, but not all regions have benefitted equally from the process and many people have been harmed (Billé, Lapeyre, & Pirard, 2012). Despite overall progress towards the global hunger reduction target of the Millennium Development Goals,[2] approximately 805 million of the world's people (11.3% of the total population) remain chronically undernourished. Nearly all of them (ca. 98%) reside in low-income areas, with at least one in four people in Sub-Saharan Africa presently lacking sufficient protein and calories for energy (FAO, 2014a). Micronutrient deficiencies, coined as 'hidden hunger', affect about two billion people worldwide, the prevalence of which is similarly highest in developing countries where dietary diversity is low and starchy staple foods predominate (Thompson & Amoroso, 2011). At the other end of the spectrum, over one billion people are overweight and 475 million are obese, with most being in the developed world (FAO, 2013). This nutritional disparity existing between the world's rich and poor is predominantly a result of social and economic factors, including the uneven distribution of global food trade (MEA, 2005).

Many individuals living in poorer countries, especially in rural areas, are often directly dependent on the extraction of wild foods from local ecosystems to bridge the hunger gap created by poverty, environmental stresses and/or civil unrest (MEA, 2005). Wild meat or 'bushmeat' (Box 1), in particular, serves as a key contributor to the food security and livelihoods of millions of individuals throughout the developing world (Brashares, Golden, Weinbaum, Barrett, & Okello, 2011). Bushmeat serves multiple roles and provides many benefits to those that use it. Most notably, this wild resource provides a crucial source of protein in places where domestic alternatives are scarce and expensive (Swamy & Pinedo-Vasquez, 2014). By some estimates, bushmeat

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[2] Millennium Development Goal, Target 1C: "to halve, by 2015, the proportion of people who suffer from hunger".

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0963-9969/

Box 1
Bushmeat — concepts and terminology.
Sources: Bennett et al. (2007), Eves & Ruggiero (2002), Nasi et al. (2008), Redmond et al. (2006), and Van Vliet (2011).

Bushmeat is defined in this paper as the meat derived from any wild terrestrial mammal, bird, reptile or amphibian harvested for subsistence or trade, most often illegally. Fish, crustaceans and molluscs are excluded from this definition and while invertebrates are recognised as important dietary items for many communities, focus is placed on the larger vertebrates that constitute the bulk of the terrestrial wild animal biomass consumed by humans.
Although the term 'bushmeat' originated from Africa, it is now widely used to describe the meat taken from wild animals across the tropics, along with other names such as game, wild meat, bushtucker or chop. Here, however, a distinction is drawn for *game meat*, with this term being reserved for the meat that is legally harvested from non-domesticated land mammals and birds, through formalised activities such as ranching, safari hunting and cropping.
In the context of this paper, there is also a need to separate out the illicit and highly-organised trade of other high-value wildlife products (e.g. rhinoceros horns, tiger bones and pangolin scales for medicinal purposes), which, while undeniably a significant threat to many high-value species, will not be dealt with in depth in this paper.

contributes 80–90% of the animal protein consumed in certain rural regions of West and Central Africa (Ntiamoa-Baidu, 1997; Pearce, 2005) and over 20% of that eaten by several indigenous groups in the Amazon (Rushton et al., 2005). Beyond its nutritional contribution, bushmeat also provides an important source of income where few alternatives exist, since it is easily traded, has a high value-to-weight ratio and can be preserved (dried) at low cost (Nasi et al., 2008). Furthermore, bushmeat is often favoured for consumption because it is familiar, traditional or since it confers social prestige (Van Vliet & Mbazza, 2011), while in many (but not all) cases it may be preferred for its taste (Schenck et al., 2006).

Humans have harvested wildlife for food for millennia, using various traditional hunting techniques to capture and kill an array of species whose habitat they shared. While human populations remained relatively small, weapons primitive and where the main goal was simply to secure sufficient food for the family or village, this hunting carried only a localised impact and was mostly sustainable (Nadakavukaren, 2011; Wilkie, Bennett, Peres, & Cunningham, 2011). In more recent times, however, the situation has changed dramatically. As human populations have continued to escalate, pressures on natural ecosystems have become progressively severe. Technological advances, infrastructure development and the loss of traditional hunting controls have facilitated the extensive exploitation of many wildlife species. Increasing urban demand for bushmeat has simultaneously catalysed a booming commercial trade, which, when combined with the latter factors, has led to harvests that are unprecedented and increasing rapidly (Milner-Gulland & Bennett, 2003; Swamy & Pinedo-Vasquez, 2014). Large-scale biodiversity loss is now globally pervasive and widely documented, with numerous case studies revealing a multitude of sites where once vibrant wildlife populations have been hunted to a state of defaunation (Brashares et al., 2011). The 'bushmeat crisis', a term coined to describe the overharvesting of wildlife for food, is now seen as the greatest threat to biodiversity in some regions, but concurrently is of the greatest threats to the livelihoods of those that depend on the resource the most (Redmond, Aldred, Jedamzik, & Westwood, 2006).

Whether and under what circumstances the future use of bushmeat will be sustainable is consequently a contentious issue (Cawthorn & Hoffman, 2014), frequently pitting conservation biologists against humanitarians in a pro-wildlife versus pro-people debate (Miller, Minteer, & Malan, 2011; Redmond et al., 2006). To date, most studies aimed at mitigating the bushmeat crisis have been rooted in the biological disciplines; a biocentric approach focused on measuring the impact of bushmeat harvesting on targeted wildlife populations. This has resulted in efforts being concentrated on the protection of the species and the criminalisation of bushmeat hunting in many countries as part of conservation policies, often in regions that were previously traditional hunting grounds (Swamy & Pinedo-Vasquez, 2014). On the other hand, comparatively little research has focused on the anthropocentric dimensions, in which bushmeat is regarded as a crucial dietary item and where declining wildlife populations are equated with the loss of human resources (Bowen-Jones, Brown, & Robinson, 2002).

The current nature and complexity of socio-ecological systems remains deeply contingent on the past. Indeed, a full appreciation of the existing situation cannot be gained without going back decades, centuries or even millennia (Costanza, Graumlich, & Steffen, 2007). Nevertheless, our priorities on sustainable development must be set in the present, with the realisation that biodiversity conservation and food security are essentially two sides of the same coin (Sunderland, 2011). Conservationists should therefore share a common concern about sustainability with human development advocates when wildlife depletions are seen to exacerbate poverty. While the integration of the social sciences into wildlife management has begun, albeit slowly, there is still a scant understanding of the economic, health and social factors driving human reliance on wildlife and dictating the sustainability of the harvest (Manfredo, 2009). This paper aims to shift the focus to the human dimension, emphasising the true contributions of bushmeat to food security, nutrition and well-being, while balancing this perspective by considering the far-reaching impacts of overexploitation.

2. Methodology

In order to investigate the extent of bushmeat use, the contribution of the resource to human livelihoods, as well as the drivers and implications of overexploitation, a comprehensive review of the literature was conducted between August 2014 and February 2015, the process of which is mapped in Fig. 1. Search terms and Boolean search operators were firstly used to explore published and peer-reviewed literature indexed in the bibliographic databases Science Direct, Google Scholar, SCOPUS, EBSCO Host and Web of Science. A general search ("bushmeat" OR "bush meat" OR "wild meat") was conducted at the outset, with the number of 'hits' in each database being recorded (Fig. 1). Due to the unmanageable number of publications returned using this strategy, more targeted searches were conducted by modifying the search strings to include keywords associated with each of the five major themes addressed in the paper (Fig. 1). The 'grey' literature was also explored using similar search terms in Google, so as to identify relevant theses and dissertations, working papers, project documents and other unpublished materials. The titles and keywords of the captured literature sources were evaluated to ascertain their relevance, where after the abstracts or executive summaries of those passing through this first review stage were further screened. More detailed review allowed refinement to 250 key literature sources, the findings of which are integrated throughout the current paper. It is important to note that, while a global outlook was sought throughout, the focus of the paper did inevitably fall on those regions in which bushmeat harvesting, consumption and trade are the highest, since this is where most research efforts have been placed to date.

3. Bushmeat harvesting and consumption

3.1. The scale of the harvest

Levels of bushmeat off-take vary considerably by continent, country and ecological zone. Nonetheless, hunting efforts tend to be concentrated

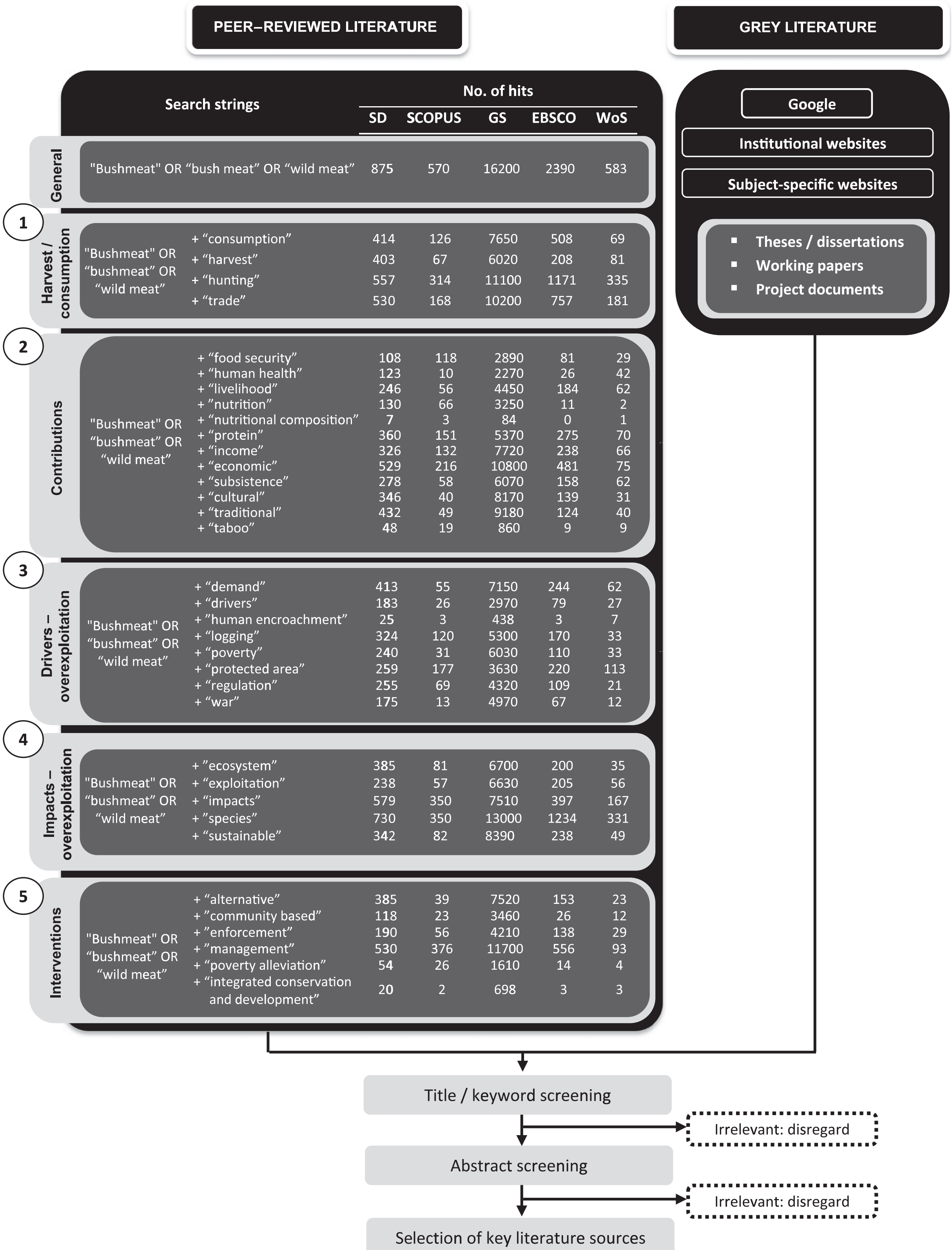


Fig. 1. Schematic map of the processes used to capture and refine key literature sources for this review, with the number of “hits” in each database for individual search strings being indicated (SD = Science Direct; GS = Google Scholar; WoS = Web of Science).

in many of the most biodiverse ecosystems in the world, which also correspond with the highest incidences of poverty and human malnutrition (Fisher & Christopher, 2006; Treweek, Brown, & Bubb, 2006). Despite being illegal in many countries (Lindsey et al., 2013), bushmeat extraction rates are by far the highest in tropical Africa, while being lower, yet still significant in Latin America and Asia (Brown, 2007). The total bushmeat harvest in the Congo basin alone is estimated at 4.5–4.9 million tonnes per annum, while the corresponding value in the Amazon basin is as high as 1.2 million tonnes per annum (Fa, Peres, & Meeuwig, 2002; Nasi, Taber, & Van Vliet, 2011). The scale of the bushmeat harvest in Asia remains largely unquantified, but the most recent estimates for the Malaysian state of Sarawak point to an annual harvest of ca. 23,500 tonnes (Bennett, 2002).

3.2. Composition of the harvest

Sources of bushmeat encompass a wide range of taxa, ranging from small minifauna to the more renowned megaherbivores. In Sub-Saharan Africa, over 500 different species of bushmeat may be consumed (Redmond et al., 2006), with at least 114 species being documented in hunter catches, markets and household consumption in Gabon alone (Abernethy & Ndong Obiang, 2010). More than 400 wild terrestrial animal species are hunted for food in South and South-Eastern Asia, while in South America this number equates to almost 200 species (Redmond et al., 2006). In both the African and Amazon tropical forests, medium-sized animals (2–50 kg) are most commonly harvested, although larger species (e.g. wild pigs, large antelope, forest buffalo, tapirs and even elephants) are taken when the opportunity arises. Although hunting efforts differ both spatially and temporarily, mammals generally make up the majority of the bushmeat harvest in terms of number and biomass, with ungulates and rodents contributing most notably (Fa et al., 2006; Taylor et al., 2015). In a series of studies conducted in West and Central Africa, ungulates and rodents comprised 73% and 12% of the total harvested biomass, respectively, while accounting for up to 42% and 39% of the carcasses appearing on local bushmeat markets (Fa, Ryan, & Bell, 2005; Fa et al., 2006, in press). The duikers (small forest antelope, *Philantomba* sp./*Cephalophus* spp.), brush-tailed porcupine (*Atherurus africanus*), cane rat (*Thryonomys swinderianus*) and giant pouched rats (*Cricetomys* spp.) generally occur most frequently in hunter off-takes and on markets in the aforementioned regions. Non-human primates (primates hereafter, e.g. monkeys, chimpanzees and apes) rarely account for more than 20% of the animals sold in African bushmeat markets, while reptiles, birds, amphibians and bats generally constitute an even lower percentage (Fa et al., 2005, 2006, in press; Van Vliet, Nasi, & Taber, 2011). Similarly, the majority of the bushmeat off-takes in the Amazon comprise medium-sized ungulates such as peccaries (*Tayassu pecari*/*Pecari tajacu*) and brocket deer (*Mazama* spp.), as well as large rodents like the paca (*Cuniculus paca*) and agouti (*Dasyprocta* spp.), but the harvesting of tapir (*Tapirus* spp., ca. 200 kg) can prove very valuable in biomass terms (Nasi, Taber, & Van Vliet, 2011; Suarez et al., 2009). Bushmeat markets in tropical North Sulawesi, Indonesia, are dominated by small-bodied mammals (47% bats, 44% rodents and 7% Sulawesi pigs — *Babyrousa babyrussa*) (Lee et al., 2005), reflecting the local declines of many larger-bodied species (Corlett, 2007).

3.3. Patterns of consumption and trade

While undoubtedly an important dietary item for many, it is now increasingly clear that the drivers and patterns of bushmeat consumption are not static. These vary not only temporarily, but also between economically disparate countries and between rural and urban areas, mainly in accordance with availability, price, disposable income and cultural preferences (Brashares et al., 2011; Fa, Currie, & Meeuwig, 2003; Kümpel et al., 2007). Rural bushmeat hunters in the Amazon consume approximately 63 kg of bushmeat per capita per annum, while those in the Congo basin, who rely almost exclusively on bushmeat for their animal protein intake, consume ca. 51 kg per capita per annum (Nasi et al., 2011). Rural consumption patterns remain similarly high in the remote forest regions of South-East Asia, where bushmeat is less than half the price of domestic meats (Swamy & Pinedo-Vasquez, 2014). Urban consumption, however, differs widely on these continents and bushmeat is not always essential for meeting basic needs. In fact, in a large-scale study carried out across four African countries (Ghana, Cameroon, Tanzania and Madagascar), Brashares et al. (2011) demonstrated that bushmeat consumption increases with household wealth in urban settings, whereas consumption is highest for the poorest households in rural settings. Thus, while urban demand may well be created at times by a lack of affordable or acceptable alternatives, very often this is driven by the wealthy elite who perceive bushmeat as a luxury item for which they are willing to pay high prices (Kümpel et al., 2007).

Most recent estimates indicate that only 5–8 million people in South America (ca. 1.4–2.2% of the total population) regularly rely on bushmeat as a protein source, with many being amongst the poorest of the region (Rushton et al., 2005). While urban bushmeat consumption on the continent has previously been considered negligible (Rushton et al., 2005), there is now some evidence to show that this situation may be changing in Amazonia's increasingly urbanising wilderness, particularly in the forested Brazilian pre-frontier cities (Parry, Barlow, & Pereira, 2014). Nonetheless, the overall situation is very different in the Congo basin, where urban consumption is widespread and significant and increases with income in certain areas (Mbete et al., 2011; Wilkie et al., 2005). Much of this urban trade occurs in open markets along with other agricultural products, but a substantial proportion of bushmeat also passes through more informal channels (i.e. sold directly from rural hunters to urban consumers). Although per-capita urban consumption in the Congo basin appears an order of magnitude lower than that for rural consumption, aggregate consumption is higher for the former than for the latter as a result of the size of the urban population (Nasi et al., 2011). It has been estimated that approximately 161 tonnes of bushmeat is sold annually in five markets in Gabon (Starkey, 2004), while the quantity traded in the four main markets of the Cameroonian capital, Yaoundé, can reach up to 1080 tonnes per annum (Bahuchet & Loveva, 1999). The commercial trade is considered as one of the primary drivers for increasing bushmeat off-takes from this region and, given the limited livestock sector in many Central African countries, the situation is likely to worsen as populations continue to grow and become more urbanised (Bennett et al., 2007). A similar trend is being seen in West, East and southern Africa, where increasing urbanisation is linked with a growing reliance on bushmeat resources (Barnett, 2000; Cowlishaw, Mendelson, & Rowcliffe, 2004; Lindsey & Bento, 2012). In South-East Asia's major consumer markets, increasing affluence has led to a spiralling demand for wildlife products, with bushmeat being consumed in sizable quantities in urban areas, generally more as a luxury than a staple food source (Bennett & Rao, 2002a).

4. Contribution of bushmeat to human livelihoods

4.1. Food security and nutritional contributions

Bushmeat makes its most significant and direct contribution to food security in places and at times when it is the only or main source of protein available, and is not easily withdrawn or replaced (Fa et al., 2015; Williamson, 2002). As previously noted, this situation potentially applies to millions of rural or forest dwellers across Africa, Latin America and Asia, who are amongst the poorest and most marginalised in their countries. This wild resource can also contribute indirectly to the food security of these people when some or all of their income is derived through the bushmeat trade, which in turn can be used to purchase other crucial food supplies (Lindsey, Romanach, Matema, et al., 2011). In order to fully appreciate the extent to which bushmeat provides for their basic needs, it is important to emphasise precisely what the term 'food security' encompasses, placing this in the context of alternative sources of subsistence, opportunities in the local economy and prevailing cultural beliefs.

Food security, according to the multi-faceted definition most widely used today (FAO, 1996), is underpinned by four critical pillars, namely availability, access, utilisation and stability (Fig. 2). Most efforts towards achieving this goal have traditionally focused on the supply side of the equation, raising the question of whether 'enough' food is available, usually interpreted in terms of dietary energy (Pinstrup-Andersen, 2009). Following this very narrow perspective, a major obstacle is already encountered in many developing countries, where a stable supply of quality food is simply not readily available to all communities. In many African regions, for instance, domestic agricultural production has been hindered by factors such as land tenure security, poor soils, high seasonal variability, the prevalence of livestock diseases such as trypanosomiasis, as well as declining local and foreign investment in the sector (Fa et al., 2003; Redmond et al., 2006). Local agricultural production provides for the needs of only 38% of the people in Gabon (total population: ca. 1.6 million people) and less than 50% in the Republic of Congo (total population: ca. 4.6 million people) (Fa et al., 2003), while domestic animal protein is similarly scare in the West African region.

Even where food does theoretically exist at the international or national levels, availability does not necessarily ensure access at the household or individual level. Indeed, the underlying reasons for food insecurity are frequently rooted in a myriad of political, economic and social constraints that preclude food attainment by vulnerable populations (Sunderland, 2011). In war-torn regions of Central Africa, for example, the degradation of roads and trading routes has impeded the transportation of bulky agricultural commodities to markets (Redmond et al., 2006). In cases where functioning markets do exist, rural dwellers may be far removed from these, often having limited transportation to permit access. The reality further remains that many poor people simply do not have the financial resources to purchase pricey domestic meat products, let alone the more expensive imported protein sources (Nasi et al., 2011). Low cost, energy-rich staple crops have consequently become a central focus of policy makers in the quest for global food security. Often overlooked, however, is that food composition is as crucial to food security and nutrition as availability and access (Sunderland, 2011). While these starchy staples may well assure caloric sufficiency, they provide small amounts of limiting nutrients per unit energy, meaning that their use alone will not satisfactorily address the malnutrition problems experienced in many developing countries (Vinceti et al., 2013).

Bushmeat, in contrast, represents an accessible and essentially 'free' source of food that can be captured rather than purchased (Kümpel, 2006). Even in substantial urban markets, such as those in the Democratic Republic of Congo (DRC), bushmeat is one of the cheapest meat sources available and constitutes the protein staple for many poorer households (Van Vliet, Nebesse, Gambalemoke, Akaibe, & Nasi, 2012). Bushmeat can be critical to human welfare throughout the year in some regions, while in others it is relied upon more heavily during certain seasons, providing a vital 'safety net' in times of economic hardship, food shortages or other emergency or external shock situations (Brashares et al., 2004; Jambiya, Milledge, & Mtango, 2007; Sunderland, 2011). Bushmeat can also prove to be an important food source for community members practicing seasonal migrant labour,

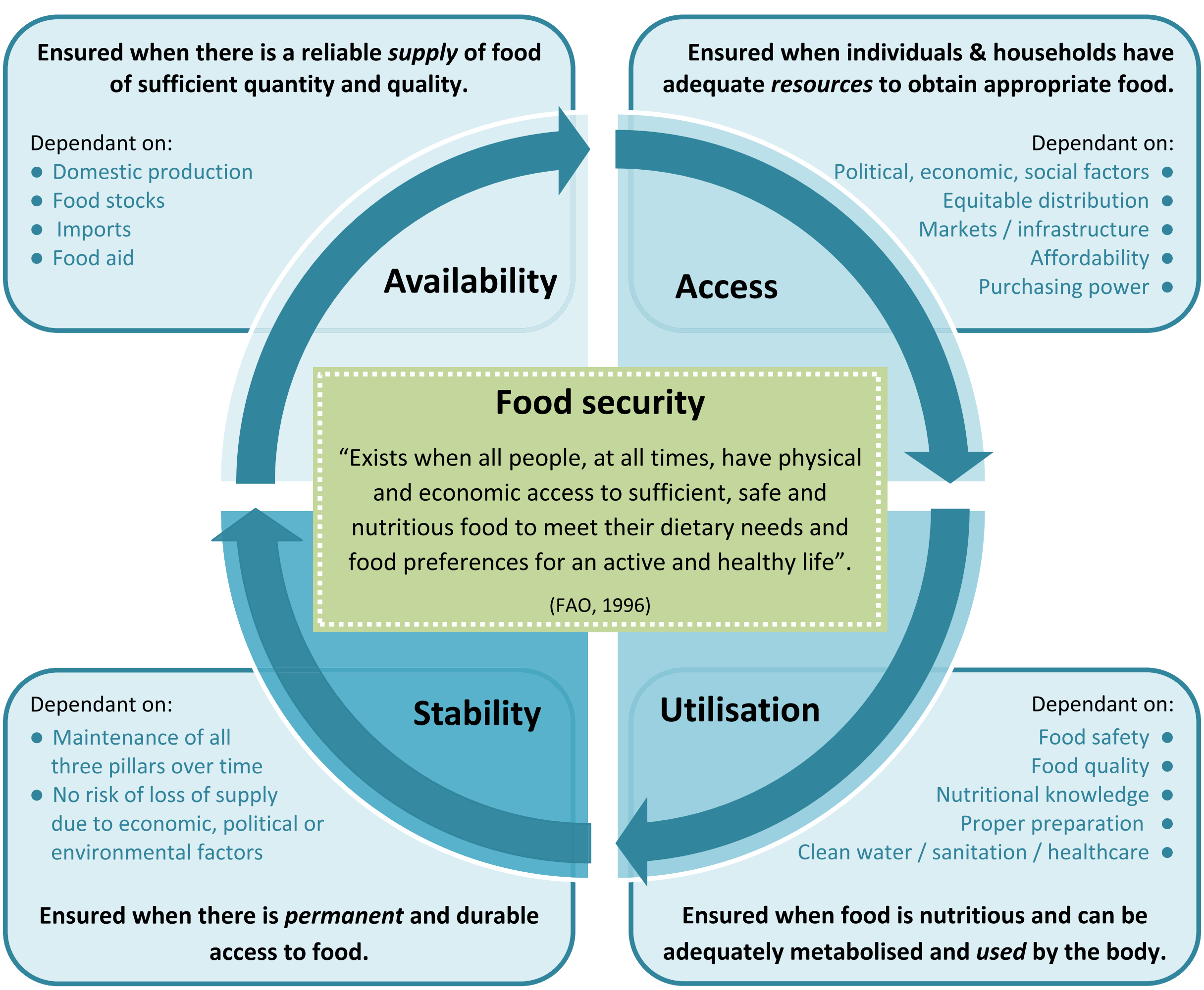


Fig. 2. The concept of food security and the inter-relationship of the four critical pillars that underpin it.

who generally have limited capacity to plant family gardens or participate in other forms of agricultural production (Rushton et al., 2005).

While the importance of bushmeat as a protein provider is well documented, relatively few studies have emphasised the overall contribution of bushmeat consumption to the basic nutrition of its consumers. This can be partially attributed to the fact that the current understanding of the macro- and micro-nutritional properties of wild foods lags far behind that of domestic livestock and cultivated crops (Vinceti et al., 2013). Nonetheless, that information that can be gleaned on the nutritional composition of bushmeat suggests that this is comparable or even superior to domestic meat sources, indeed being high in protein, as well as readily assimilable amino acids and essential fatty acids (Strazdiòa, Jemeïjanovs, & Đterna, 2013). Collation of the available proximate composition data for a number of bushmeat species consumed in different regions (Table 1) indicates that protein values range from 17 to 26% in the meat from African antelope species through to 28% and 45% in smoked cane rat (*T. swinderianus*) and porcupine (*Hystrix africaeaustralis*) meat, respectively.

Nasi et al. (2011) examined data from several studies on rural bushmeat consumption in the Amazon and Congo basins to arrive at average estimates of ca. 172 g- and 140 g-per capita per day for the two locations, respectively. More specifically, bushmeat consumption in Gabon has been estimated at 80 g per average male equivalent (AME)[3] per day, although rural consumption can be considerably higher (≥260 g/AME/day; 74% of total animal protein intake) than urban consumption at some locations (20–120 g/AME/day; 4–41% of total animal protein intake) (Starkey, 2004; Wilkie et al., 2005). A 75-kg adult male requires around 50 g of protein per day for optimal health (FAO/WHO, 2007), albeit that this may vary with nutritional status and diet quality. Taking a modest average protein content in bushmeat of 20%, this wild resource could consequently contribute more than 100% and up to 48% of the daily protein requirements in Gabon's rural and urban locations, respectively. While figures are somewhat dated, Anstey (1991) estimated rural bushmeat consumption for Liberia (West Africa) to be in the order of 288 g per capita per day, with such contributions likely to far exceed the recommended daily requirements for protein.

Aside from protein, the supply of calories from bushmeat should not be discounted, especially in cases when few alternative energy sources are available for consumption. While some bushmeat species are relatively low in fat (<5%, e.g. monkeys, hares, most antelope) (Smil, 2002), others such as rodents have higher lipid contents and energy densities, and are valued for their fatty consistencies (Hoffman & Cawthorn, 2012). Furthermore, bushmeat provides several important micronutrients (vitamins and minerals), generally in higher quantities and with higher bioavailability than those found in plant foods (Golden, Fernald, Brashares, Rasolofoniaina, & Kremen, 2011; Vinceti et al., 2013). Micronutrients are crucial for health and developmental functions, with deficiencies manifesting in a range of health sequela. Notably, deficiencies in iron, zinc and vitamin B12 are known to impair growth and cognitive development, with life-long ramifications on both health and socio-economic success. Animal foods, such as bushmeat, apart from offering a more varied diet, are amongst the best sources of the latter nutrients, as well as regularly being the only dietary sources of Vitamin D and retinol (Vinceti et al., 2013).

In many parts of Africa, climate-induced vulnerabilities (e.g. drought) and the rising prevalence of HIV/AIDS have led to significant declines in food security, with the two working in tandem to perpetuate poor harvests and reduced incomes (Bharucha & Pretty, 2010). For poor households afflicted by HIV/AIDS, bushmeat offers a nutritious dietary supplement at low financial and labour costs. The contribution of this wild resource to food security becomes even more critical when considering that deficiencies of micronutrients required for immune functions are frequently observed for those living with HIV/AIDS (Piwoz & Bentley, 2005). A number of studies conducted in South Africa demonstrate that bushmeat consumption is more likely in certain HIV/AIDS-afflicted households (Abu-Basutu, 2013; Kaschula, 2008). Increased vulnerability to HIV/AIDS has also been shown to increase the reliance of rural African children on wild foods, with afflicted children at some sites obtaining a significantly ($p < 0.001$) higher proportion of meat from the wild in comparison to non-afflicted children (McGarry, 2008).

Despite its nutritional contributions, it is important to note that there are also some serious health concerns associated with the consumption of bushmeat. Up to 75% of emerging infectious diseases in humans are of zoonotic (animal) origin, most of which originate in wildlife. The hunting and butchering of bushmeat, particularly primates, have been implicated in the transmission of several zoonotic pathogens to humans, including simian immunodeficiency virus (SIV, zoonotic form of HIV), Ebola, severe acute respiratory syndrome (SARS), monkeypox, simian T-lymphotropic virus and simian foamy virus (Smith et al., 2012). Fruit bats, also a reservoir for the Ebola virus, are believed to be responsible for the current (2013–2015) Ebola outbreak in West Africa, although this has not been corroborated (Bausch & Schwarz, 2014). Nonetheless, the zoonotic potential of bushmeat is often not well recognised amongst those that consume it, with bushmeat rather being perceived as healthy, tasty and/or part of the cultural heritage (Kamins et al., in press; LeBreton et al., 2006; Subramanian, 2012).

4.2. Economic contributions

Most rural people living at the margins of the cash economy have very limited options for generating an income. They often lack the capital to invest in livestock husbandry, as well as the education and skills to find suitable and permanent employment (Fa & Brown, 2009). Without access to land or markets, the harvesting of wildlife resources generally offers the greatest return on labour input, with few barriers to entry and minimal start-up costs (Brown, 2007). Thus even where bushmeat is utilised to meet basic needs, many communities also rely on hunting to supplement their short-term cash requirements, with the distinction between subsistence and commercial use often being blurred (Kümpel, Milner-Gulland, Cowlishaw, & Rowcliffe, 2010). For them, bushmeat sales afford a means to purchase items and materials that a subsistence lifestyle does not provide. This is exemplified by the response of a 23 year-old Zambian man, 6th-grade education, when questioned about his motives for hunting: “You asked about the difference between poachers and those who don't poach? Those who don't poach are poor. They don't have soap and other necessities” (Brown & Marks, 2007).

For some, the trade in bushmeat can represent a full-time source of income, while for others this may serve as a buffer during times of hardship (e.g. crop failure, unemployment, illness of relatives) or as a means to generate extra cash for special needs (school fees, funerals) (Fa & Brown, 2009; Nasi et al., 2008). The decision to consume or trade bushmeat depends on prevailing economic and nutritional statuses, alternative opportunities for income and food generation, as well as the potential value of the harvested commodity (Milner-Gulland & Bennett, 2003). In some cases, as hunting off-takes increase so too does the proportion of bushmeat sold, indicating that residual meat is traded only once the protein needs of the household are fulfilled. In the Serengeti, most people (75%) hunt to fulfil their protein requirements, with fewer being motivated by income (Mfunda & Røskaft, 2010). In contrast, while bushmeat contributes moderately to the diets of poor households in the DRC and more so in the lean season, by far the majority is sold to produce a much needed source of cash revenue (de Merode, Homewood, & Cowlishaw, 2004). A similar pattern has been documented for rural hunters in Equatorial Guinea (Kümpel et al., 2010) and in Cameroon (Wright & Priston, 2010).

[3] AME (average male equivalents) is a measure used to control for demographic compositions of households and, when used to express nutritional data, is generally calculated based on estimated daily food energy requirements of individuals of different age and gender (see also Wilkie et al., 2005).

Table 1
The proximate composition (per 100 g) of the raw or smoked meat of some bushmeat species consumed in the developing world compared with domestic livestock species.

Animal species		Moisture (g/100 g)	Protein (g/100 g)	Fat (g/100 g)	Ash (g/100 g)	Energy (kcal)	Calcium (mg/100 g)	Phosphorus (mg/100 g)	Iron (mg/100 g)	Reference
Mammalia										
Buffalo — African (smoked)	*Syncerus caffer*	61.2	34.5	2.3	1.7	168.0	60.0	120.0	6.0	Malaisse (2010).
Bushbuck (smoked)	*Tragelaphus scriptus*	51.9	41.9	1.1	1.7	189.0	25.0	320.0	15.0	Malaisse (2010).
Duiker — blue	*Philantomba monticola*	72.0	22.0	3.1	1.4	122.0	–	–	–	Malaisse (2010).
Duiker — common	*Sylvicapra grimmia*	71.4	25.7	2.1	1.3	–	30.8	476.7	14.3	Hoffman and Ferreira (2004).
Eland (smoked)	*Tragelaphus oryx*	66.0	29.2	0.4	1.3	128.0	60.0	210.0	7.0	Malaisse (2010).
Grysbok — Sharpe's	*Raphicerus sharpei*	73.3	19.7	4.4	1.1	121.0	20.0	160.0	8.0	Malaisse (2010).
Hartebeest — red	*Alcelaphus buselaphus*	75.0	23.3	0.6	1.2	–	–	–	–	Hoffman, Smit, and Muller (2010).
Impala	*Aepyceros melampus*	75.0	22.6	2.1	1.2	–	6.3	149.7	2.4	Hoffman, Mostert, Kidd, and Laubscher (2009).
Klipspringer (smoked)	*Oreotragus oreotragus*	27.0	1.9	1.4		132.0	30.0	260.0	7.0	Malaisse (2010).
Kudu — greater	*Tragelaphus strepsiceros*	75.7	22.8	1.5	1.2		9.7	162.8	2.2	Hoffman et al. (2009).
Reedbuck — southern (smoked)	*Redunca arundinum*	52.5	42.0	4.2	1.4	217.0	25.0	400.0	5.0	Malaisse (2010).
Sitatunga (smoked)	*Tragelaphus spekii*	58.0	36.0	1.7	1.2	169.0	60.0	350.0	7.0	Malaisse (2010).
Waterbuck (smoked)	*Kobus ellipsiprymnus*	41.1	52.0	1.7	1.4	237.0	5.0	420.0	8.0	Malaisse (2010).
Hippopotamus (smoked)	*Hippopotamus amphibius*	48.2	32.6	13.8	1.3	264.0	20.0	100.0	10.0	Malaisse (2010).
Collared peccary	*Tayassu tajacu*	71.2	19.6	8.0	0.8	–	–	–	–	Saadoun and Cabrera (2008).
Desert warthog (smoked)	*Phacochoerus aethiopicus*	51.5	43.0	3.7	1.8	217.0	60.0	300.0	8.0	Malaisse (2010).
Red river hog (smoked)	*Potamochoerus porcus*	41.3	45.9	2.3	1.9	217.0	40.0	300.0	6.0	Malaisse (2010).
Zebra	*Equus burchelli*	75.2	22.8	0.3	1.5	–	–	–	–	Onyango, Izumimoto, and Kutima (1998).
African elephant (smoked)	*Loxodonta africana*	64.5	31.2	2.4	1.1	155.0	10.0	215.0	7.0	Malaisse (2010).
Blue monkey	*Cercopithecus mitis*	72.6	21.4	3.0	1.3	118.0	–	–	–	Malaisse (2010).
Vervet monkey	*Chlorocebus pygerythrus*	69.5	23.7	1.2	1.4	112.0	–	–	–	Malaisse (2010).
Yellow baboon	*Papio cynocephalus*	71.2	22.3	3.7	1.8	112.0	–	–	–	Malaisse (2010).
Thick-tailed greater galago	*Otolemur crassicaudatus*	68.6	20.7	9.4	1.3	173.0	160.0	200.0	–	Malaisse (2010).
Rodentia										
African giant rat	*Cricetomys gambianus*	65.4	20.1	11.4	2.0	–	50.0	750.0	73.0	Oyarekua and Ketiku (2010).
Greater cane rat (smoked)	*Thryonomys swinderianus*	52.0	28.0	16.8	2.9	271.0	320.0	380.0	20.0	Malaisse (2010).
Tree squirrel	*Paraxerus cepapi*	74.3	21.0	3.2	1.5	119.0	230.0	250.0	5.0	Malaisse (2010).
Cape porcupine (smoked)	*Hystrix africaeaustralis*	48.0	45.8	4.1	1.7	233.0	150.0	310.0	5.0	Malaisse (2010).
Nutria/coypu (wild)	*Myocastor coypus*	75.7	22.1	1.3	1.0	–	5.2	–	1.7	Tulley et al. (2000).
Reptilia										
Iguana	*Iguana* spp.	74.7	20.8	3.49	1.2	–	–	–	–	De Moreno et al. (2000).
Argentine giant tegu	*Tupinambis merianae*	72.0	23.6	4.0	1.2	–	–	–	–	Caldironi and Manes (2006).
Nile crocodile	*Crocodylus niloticus*	71.64	22.08	6.23	0.51	–	6.8	193.9	0.3	Hoffman, Fisher, and Sales (2000).
Domesticated species										
Cow (beef), lean	*Bos* spp.	73.1	23.2	2.8	–	119	4.5	215.0	1.8	Williams (2007).
Sheep (mutton), lean	*Ovis aries*	73.2	21.5	4.0	–	122	6.6	290.0	3.3	Williams (2007).
Goat	*Capra hircus*	75.99	18	2.51	1.38	–	–	–	–	Arain et al. (2010).
Domestic pig	*Sus scrofa domesticus*	75.51	21.79	2.02	0.99	154.5	–	–	0.4	Kim et al. (2008).

Bushmeat commodity chains can be complex, at times including just the hunter and close neighbours, but at others stretching through to traders along major transport routes, to market stall owners and roadside restaurants, and ultimately to urban consumers (Swamy & Pinedo-Vasquez, 2014). The number of middlemen and re-sellers is, however, small in comparison to the number of hunters and the majority of the generated income is retained in the hands of the primary producer (the hunter) (Brown, 2007). For instance, hunters are reported to capture 74% of the final sales price of bushmeat traded in the urban markets of Takoradi, Ghana (Cowlishaw et al., 2004). Nevertheless, the way in which this income is spent inevitably determines its potential for poverty alleviation. Studies in Cameroon, Gabon and Equatorial Guinea indicate that much of hunter's incomes tend to be spent on non-essential items (e.g. alcohol and cigarettes) (Coad et al., 2010; Kümpel et al., 2010; Solly, 2004), although this pattern is not fundamentally different from that seen for income generated through other activities.

4.3. Cultural contributions

Hunting and the consumption of bushmeat are integral parts of the cultural heritage of many indigenous communities, often being closely linked with social status and the maintenance of ancestral ties. In parts of Africa, hunters hold esteemed status since they provide food for female-led households and the elderly, and are likely to be preferred by women (Barnett, 2000; Lowassa, Tadie, & Fischer, 2012). The consumption of bushmeat is also frequently associated with traditional ceremonies and rituals, such as burials in Cameroon and men's circumcision ceremonies in Gabon (Van Vliet & Mbazza, 2011; Van Vliet & Nasi, 2008). Bushmeat is further sought after by many urban elite as a means to retain links with a traditional village lifestyle (Redmond et al., 2006).

At the same time, the traditions, beliefs, values and norms of some tribes, clans, households or individuals may dictate strong preferences or prohibitions on the hunting and consumption of certain bushmeat species. The flesh of lions or leopards, for instance, may be eaten by the men of particular tribes in Eastern Africa with the belief that they will be imbued with the courageous and fierce characteristics of the consumed animal (Frazer, 2012). Similarly, the flesh of the elephant is thought by the Ewe tribe of West Africa to make the consumer strong (Frazer, 2012), while the trunk is alleged by the Wataturu tribe of Tanzania to improve male virility (Ceppi & Nielsen, 2014). Conversely, specific wildlife species may variously be regarded as symbols of power, spiritual guiders and/or the residence of ancestors (i.e. totems), with such animals being considered sacred and consequently being forbidden (taboo) to hunt or consume (Mbotiji, 2002; Obioha et al., 2012). For example, the leopard is the protected totem animal of the Bretuo clan of Ghana (Ntiamoa-Baidu, 1997) and the Mbutis of the DRC (Colding & Folke, 2001), while people believing in the human-gorilla totemic kinship in Cameroon do not eat gorilla meat (Etiendem, Hens, & Pereboom, 2011). More generalised species-specific taboos also exist for different clans, with the reasons for avoidance including tradition, an animal's perceived toxicity, as well as its physical or behavioural characteristics (Colding & Folke, 2001). In parts of Equatorial Guinea, certain primates are taboo due to their resemblance with humans, the bushbaby (*Galago* spp.) is avoided as it is thought to be evil, the African palm civet (*Nandinia binotata*) and crowned guenon (*Cercopithecus pogonias*) are believed to make women infertile, while some reptiles are traditionally reserved for consumption by elders (Kümpel, 2006). Similarly, both the tapir (*Tapirus bairdii*) and the red brocket deer (*Mazama americana*) have traditionally been taboo amongst the Achuar people of Amazonia (Colding & Folke, 1997), although restraint towards bagging these species appears to have declined in more recent years (Chacon, 2011).

5. Drivers of over-exploitation

The reasons for bushmeat overexploitation are manifold and these can vary considerably between regions. Nonetheless, increasing human populations and widespread economic and social inequalities typically represent the root causes, many of the drivers discussed here signify the symptoms and the on-going devastation of wildlife populations is typically the outcome. Fig. 3 presents the complex web of some of these interactions, as well as their cascading effects on bushmeat demand.

5.1. Primary drivers

5.1.1. Human encroachment on vulnerable wildlife areas

The number of areas where wildlife can be sustainably harvested is limited first and foremost by their biological supply (productivity). Tropical forests, despite being significant reservoirs of terrestrial biodiversity, are in fact relatively low-productivity ecosystems, with mammalian biomass often an order of magnitude lower than that in more open savannas (Bennett et al., 2007). While large biophysical variations exist between tropical forest locations, best current estimates indicate that the vertebrate biomass production in these regions is in the order of 150 kg/km^2/annum (Robinson & Bennett, 2000). Based on this figure, it appears that these fragile ecosystems can support the nutritional needs of 1–2 person(s)/km^2 if they rely exclusively on bushmeat for protein (Nasi et al., 2008; Robinson & Bennett, 2000), although certain authors suggest this carrying capacity to be somewhat higher (Fa et al., 2002). Nevertheless, population densities in the remaining forests are estimated at 24 persons/km^2 in both the Amazon and Congo basins, and at 121 persons/km^2 in the South-East Asian forests (FAO/ITTO, 2011). Even though the populations are unequally distributed and not all people eat bushmeat, conventional wisdom and the prevailing literature tells us that both bushmeat demand and the rates of forest loss increase with the number of people (Redmond et al., 2006). Indeed, annual harvesting rates in these same forests are substantially higher than the aforementioned productivity estimate (150 kg/km^2), with values ranging from 200 to 700 kg/km^2 across several sites (Nasi et al., 2008).

One of the primary motivators for human population influxes and uncharacteristically high densities in forested areas lies with the expansion of extractive industries, which in turn is explicitly interlinked with both deforestation and defaunation (Redmond et al., 2006). Amongst these industries, commercial logging is of the most extensive across the tropics, with logging concessions occupying up to 45% of Central Africa's remaining forests (Laporte, Stabach, Grosch, Lin, & Goetz, 2007). Logging operations move like a wave over the landscape, ushering in a domino effect of events that alter ecosystems, exacerbate the impacts on wildlife species and greatly amplify the scale of the bushmeat harvest. These activities cause widespread forest fragmentation, cutting networks of roads into previously inaccessible tropical expanses and opening them up to hunters equipped with modern weapons (Abernethy, Coad, Taylor, Lee, & Maisels, 2013; Poulsen, Clark, & Bolker, 2011; Wilkie, Shaw, Rotberg, Morelli, & Auzel, 2000). The growing local economy and establishment of camps and villages around concessions simultaneously triggers the immigration of large numbers of workers, job seekers, hunters, traders and their families into once undisturbed areas (Poulsen, Clark, Mavah, & Elkan, 2009). Since industrial logging mostly occurs in remote areas and food is seldom provided to the workforce, these growing communities generate a huge local demand for bushmeat and create an in-situ market for hunters to sell their catch. In the northern Republic of Congo, for instance, the development of commercial logging operations resulted in a 64% increase in the population of logging towns, with a concurrent 64% growth in bushmeat supply (Poulsen et al., 2009). Logging practices not only result in intensified bushmeat consumption within concession areas, but increased forest access and the availability of transport expedites the supply to urban markets. Bushmeat consequently becomes a valuable market commodity, transforming a subsistence activity into a commercial one.

Elsewhere in Central Africa, wildlife has faced similar pressures due to the intensive mining for ‘coltan’ (columbo-tantalite), a tantalum-containing ore used in the capacitors for mobile phones, laptops and other portable electronic devices (Nadakavukaren, 2011). Increasing demand for electronic products at the turn of the century led to a tantalum-supply shortfall, precipitating a boom-and-bust cycle of panic buying and price increases (Hayes & Burge, 2003). Thousands of peasant farmers were consequently lured into mining, most notably in the rebel-held areas of the DRC, where anarchy prevailed and bushmeat provided the sustenance of the workers. As a result, the hunters providing the mining camps proceeded to kill off large numbers of wildlife species, including antelope, buffalo, elephants and endangered primates (Nadakavukaren, 2011). While a slump in the demand for coltan has been witnessed in more recent years, this remains a key resource in the eastern DRC where conflict between different warring factions prevails. The oil industry is reported to further contribute to the rampant overexploitation of forest-dwelling species, by establishing worker villages and increasing access to remote areas (Thibault & Blaney, 2003).

In efforts to conserve biodiversity, numerous African countries have designated vast proportions of their total land surface as protected areas, including the establishment of national parks and wildlife sanctuaries (Lindsey et al., 2014). While undoubtedly well-intentioned, this explosion of land protection is often criticised for negatively impacting on local communities through, amongst others, exclusion from natural

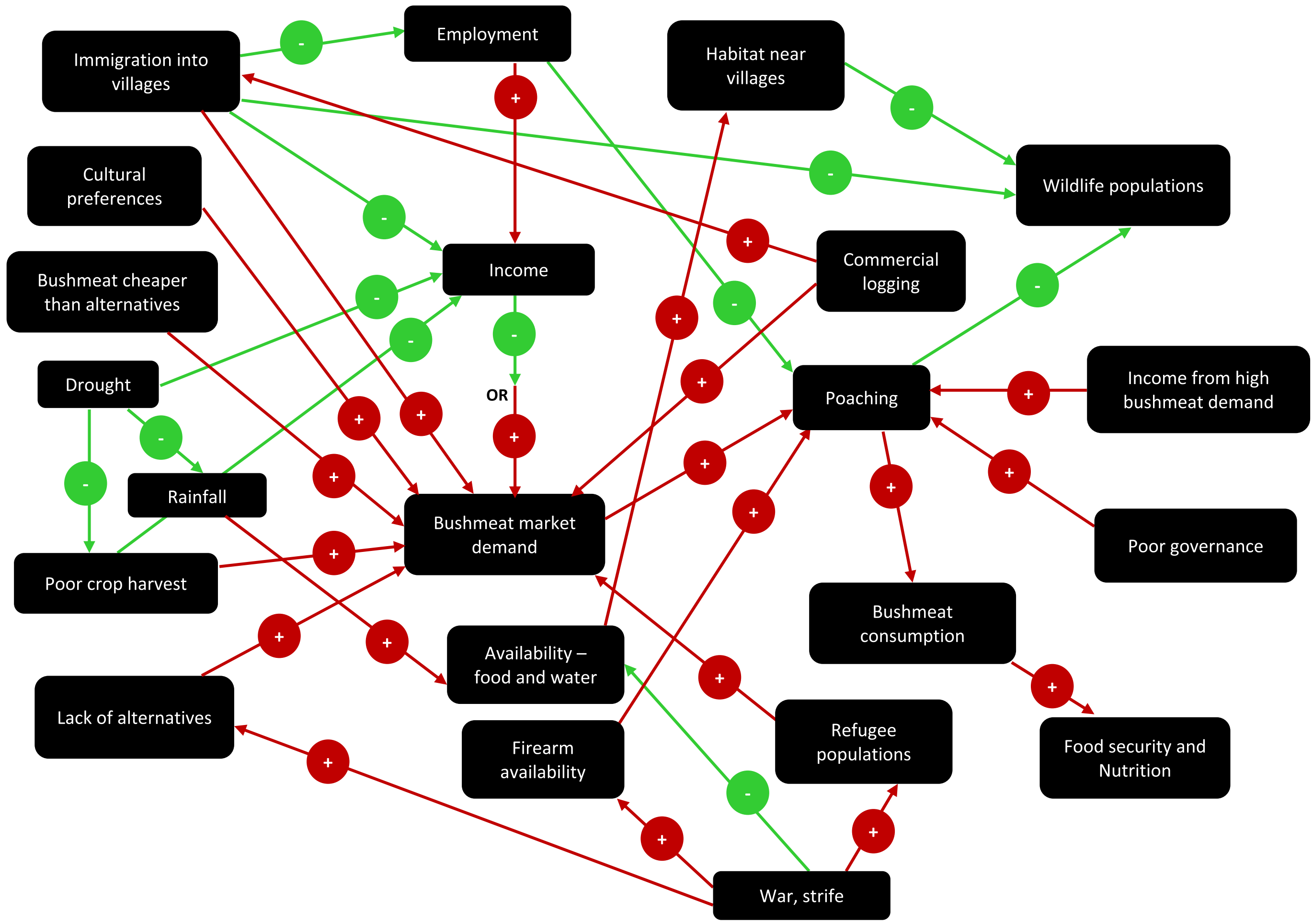


Fig. 3. The complex web of factors contributing to increased bushmeat demand and consequent resource overexploitation (arrows with + signs indicate positive relationships between components, while lines with − signs indicate negative relationships between components).

resources, loss of rights, as well as displacement from traditional lands (Cernea & Schmidt-Soltau, 2006; Roe & Elliott, 2006). While this valid argument is not in contention, it is nevertheless necessary to note that human encroachment on these protected areas is increasing in accordance with human population growth, as is the scale of bushmeat hunting (Lindsey et al., 2013). Although human settlement is not permitted within most national parks, wildlife exploitation has been particularly prominent in those where this settlement is either allowed or tolerated, such as in parts of Ethiopia, Mozambique, Tanzania and Zambia (Lindsey et al., 2014). Human population growth rates are also generally high in buffer zones or on the boundaries of national parks where settlement is mostly permitted. However, since few livelihood opportunities or functioning mechanisms exist to allow these mostly poor communities to legally benefit from the wildlife within the protected areas, poaching both within the buffer zones and the parks is often severe (Lindsey et al., 2014; Wittemyer, Elsen, Bean, Burton, & Brashares, 2008).

5.1.2. Increased urban demand and commercial trade

Urban areas of the world have continued to grow rapidly, partly due to the increasing incorporation of rural populations. At present, the urban population accounts for 54% of the total global population, a rise from 34% in 1960 (UNDESA, 2014). Most of this urban growth has been concentrated in less developed regions, with Africa and Asia urbanising more rapidly than anywhere else in the world. Over the next four decades, the urban population is projected to increase by at least two thirds, with 90% of this growth set to take place in the urban regions of Africa and Asia (UNDESA, 2014). The pervasive increase in the supply of bushmeat to urban markets, combined with human population growth projections, indicates that the aforementioned demographic shifts will have a tremendous impact on bushmeat harvests in subsequent decades. As noted previously, the urban demand for bushmeat as a luxury commodity is escalating and this is only expected to intensify in step with economic growth (Drury, 2011). This demand strengthens links between hunters and traders and has a tremendous impact on the species targeted by hunters (Swamy & Pinedo-Vasquez, 2014), with some urban traders even pre-financing hunters through the provision of ammunition supplies. The rapidly expanding luxury market has made commercial hunting more important than subsistence hunting in many cases, with rural hunters compromising their own wildlife resources to subsidise the protein consumption of the urban elite (Bennett et al., 2007; de Merode et al., 2004).

Bushmeat demand has also become a problem on a global scale, with a portion of the harvest (albeit small) entering international markets. Although quantitative data relating to the international trade is limited, it is not uncommon for bushmeat to be seized from airports across Europe and the US, posing a considerable risk for zoonotic disease transmission (EFSA, 2014; Rodríguez-Lázaro et al., 2014; Schoder et al., 2014; Smith et al., 2012). The total annual inflow of illegal bushmeat in passenger luggage to major airports in France and Switzerland has been estimated at 273 tonnes and 8.6 tonnes, respectively, with the majority originating from Central and West African countries to supply a lucrative organised trade (Chaber, Allebone-Webb, Lignereux, Cunningham, & Rowcliffe, 2010; Falk et al., 2013).

5.1.3. Unemployment, poverty and strife

Although hunting is a traditional subsistence activity for various communities, many commercial hunters have turned to this alternative only after being made redundant. Economic crisis and collapsing commodity prices for several crops (e.g. cocoa and coffee) in the late 1990s not only forced many rural farmers to seek alternative revenues, but also drove many jobless urbanites straight to the forests (Nadakavukaren, 2011). Faced with family responsibilities and few other options for food or revenue, many of these reverted to bushmeat hunting as either their temporary or full-time source of income.

Wars, civil unrests and other emergencies that generate refugee populations have a further profound effect on the scale of the bushmeat harvest (Nackoney et al., 2014). Unfortunately, these situations are not uncommon; in the year 2000, 18 Sub-Saharan countries were either in the midst of conflict or emerging from it (Gurr, Marshall, & Khosla, 2000). Human populations displaced by hostilities become heavily dependent on bushmeat as a result of their dire nutritional status and lack of alternative options (de Merode & Cowlishaw, 2006; Loucks et al., 2009). In Mozambique, for instance, wildlife resources were demolished by bushmeat hunters both during and after the civil war (1977–1992) (Hatton, Couto, & Oglethorpe, 2001). The mining of coltan is reported to have helped fund the civil wars in the DRC (1996–2003), which subsequently led to the collapse of both transport routes and food supplies to many vulnerable communities (Draulans & Van Krunkelsven, 2002; Redmond et al., 2006). With the increased circulation of arms and ammunition in the DRC, urban sales of protected wildlife species from Garamba National Park rose dramatically (de Merode & Cowlishaw, 2006). A sizable illegal bushmeat trade has also arisen in Tanzania due to the influx of refugees from neighbouring DRC, Burundi and Rwanda, largely since virtually no other protein sources exist in the encampments (Jambiya et al., 2007).

5.1.4. More sophisticated hunting technologies

As the demand for bushmeat has amplified, the increased employment of more sophisticated hunting technologies has largely reduced the traditional constraints on wildlife exploitation and decreased the probability that this will be sustainable (Nasi et al., 2008). The use of illegal snares is generally the cheapest, easiest and most pervasive means of bushmeat hunting in African forests and savannas, responsible for the extraction of the majority of wildlife species and biomass (Fa & Brown, 2009; Lindsey et al., 2013). While snares can be made from natural fibre or nylon, the increasing availability of wire from fencing, telephone or electricity cables, burnt tyres or bicycle brakes has allowed hunters to produce copious numbers of snares easily and cheaply (Becker et al., 2013; Lindsey, Romanach, Matema, et al., 2011; Lindsey, Romanach, Tambling, Chartier, & Groom, 2011). Snares are unselective, capturing virtually all species of forest wildlife and frequently killing non-target species (Becker et al., 2013). The failure of hunters to check their snares regularly also leads to enormous amounts of wastage, due to animals decomposing, being scavenged or escaping with debilitating or lethal injuries (Kümpel, 2006; Lindsey et al., 2013). Other hunting methods, such as gin traps, nets and dogs are also regularly employed by hunters in Africa (Fa et al., 2005; Gandiwa, 2011; Lindsey et al., 2013). Furthermore, the use of poisons to kill wildlife, particularly pesticides, is increasing in many regions on the continent (Ogada, 2014). While frequently representing the method of choice for killing damage-causing animals or species for their high-value products (e.g. ivory, rhino horn, fur), poisoning is additionally used as a means to harvest bushmeat for human consumption (Kissui, 2008; Muboko et al., 2014; Ogada, 2014). One survey in Ghana revealed that over 30% of bushmeat entering local markets was derived through poisoning, with pesticide residues being detected in the meat by laboratory analyses (FAO/CIG, 2002). Poisoning methods not only pose a substantial risk to human health, but can also have deleterious impacts on non-target species (e.g. hyenas and vultures) that feed on the poisoned carcasses (Gandiwa, 2011; Ogada, 2014). Firearms (mostly unlicensed) are typically reserved for the hunting of arboreal species in Africa, but are secondary in importance compared to trapping methods due to their higher costs. As the catch per unit effort from snaring decreases in a region, however, hunters are more likely to turn to firearms, which consequently pose a greater threat to endangered species, such as primates (Fa & Brown, 2009; Kümpel, 2006).

By contrast, snare hunting is virtually absent in the Amazon forests, likely since the lower populations densities documented for native forest mammals render this method relatively unsuccessful (Fa & Brown, 2009). While some indigenous groups in the Neotropics still rely on the use of blow pipes, bows and arrows and nets to capture their prey, there has been an almost universal exchange of traditional weapons with firearms across most areas during recent decades. Shotguns have a wider target area and a longer range than the aforementioned traditional methods, greatly increasing the variety of target species that can be harvested (Espinosa, 2008; Godoy et al., 2009; Jerozolimski & Peres, 2003).

5.2. Synergistic factors contributing to the unsustainable harvest

5.2.1. Nature of the resource

Bushmeat hunting is often the only means by which poor and marginalised communities can access benefits from wildlife. Nonetheless, the very nature of this resource – a common and free commodity, easily accessible and challenging to monitor – represents one of the primary reasons for its overexploitation (Nasi et al., 2008). To date, most models of wildlife management in regions where alleged overexploitation exists have tended to favour the exclusion of the users from the resource and the renunciation of its local benefits (Inamdar, Brown, & Cobb, 1999). As a result, these same users are provided with little incentive and limited capacity to manage wildlife sustainably. Low ownership and a lack of clear user rights over both land and wildlife are amongst the main factors that mutually diminish the incentive for sustainable use. With some exceptions (e.g. private landholders, see Lindsey et al., 2013), wildlife in most countries is generally considered as 'res nullius' (without ownership) or as the property of the state. Furthermore and as eluded to in Section 5.1.1, the discourse of biodiversity conservation often tends to equate low-density, sedentary human populations ('true owners') with a lack of legitimate rights, a misperception that easily justifies the transfer of rights away from these people (Inamdar et al., 1999). Alienating people from the benefits of wildlife often precipitates strained relations with the wildlife sector, frequently worsened through historical land grievances, human–wildlife conflict and heavy-handed anti-poaching tactics (Lindsey et al., 2013). Adding to this is that wildlife exploitation is in itself often prone to blanket criminalisation; an intervention that only raises resistance and discourages regulation. In many cases, the hunting of bushmeat may well represent a form of protest; persons choosing to hunt illegally are not only acquiring the benefits from the harvested animal, but they may concurrently and implicitly be making the statement that they have the right to kill this animal (Holmes, 2007).

5.2.2. Eroding traditional constraints

Long before statutory conservation policies became commonplace, local communities managed their wildlife resources through customary rules, such as the designation of species-specific taboos and sanctions for those that violated these prohibitions (Bokhorst, 2010; Obioha et al., 2012). While not always intended for conservation purposes, such taboos provided local protection to certain species, as well as to their habitats in certain cases (Colding & Folke, 2001). Nonetheless, with impinging outside influences, poverty and the growing scarcity of preferred wildlife species, many of these taboos are now being disregarded and traditional resource management systems are collapsing (Kümpel, 2006). This dynamic is exemplified in Ghana, where species previously regarded as totems, such as buffalo (*Syncerus caffer*) and crested porcupine (*Hystrix cristata*), now appear openly on major bushmeat markets (FAO/CIG, 2002). Additionally, hunters in the Luangwa Valley of Zambia are increasingly turning their attention to once taboo species such as zebras and hippos, as harvests of preferred species such as buffalo have declined (Barnett, 2000).

5.2.3. Weak governance and civil insubordination

In terms of the more formal government arrangements, hunting rules and regulations exist in almost all countries where bushmeat is harvested and traded. In virtually all of Amazonia, hunting is forbidden (except for sport hunting), yet the activity persists on a large scale either because the legislation is ignored by wealthy game hunters or because this fails to address the basic needs of the very poor (Nasi et al., 2008). In many African countries, hunting is authorised for licence holders, but restrictions are generally in place in terms of the hunting locations, seasons, species, bag limits and methods used (Lindsey et al., 2013). Hunting laws in Central Africa recognise the user rights of the local people, thus permitting traditional hunting and fishing (Nasi et al., 2008). However, most laws in Africa (including Central Africa) prohibit, inter alia, night hunting and the use of metallic snares, nets, traps (except Cameroon), poison and fire. While hunting is thus not illegal per se, poaching and the large majority of bushmeat hunting practiced in Africa contravene the aforementioned legislation (i.e. hunters seldom hold licences, hunting at night is common, nets, traps, poison and fire are used and wire is the favoured material for snares) (Lindsey et al., 2013).

Poor governance and corrupt administration prevail in most regions where bushmeat is hunted and even while laws are present, the political will, financial resources or expertise required to effectively enforce them are mostly absent (Corlett, 2007; Parry et al., 2014; Robinson, Kumar, & Albers, 2010). Wildlife policies are rarely regarded as mandatory and hunters worry little about breaking the rules, especially when there are numerous officials involved in the trade or willing to capitalise on it by accepting bribes (Bouché et al., 2012; Nielsen & Meilby, 2015). In addition, bushmeat hunters are seldom apprehended. Even if they are, the non-existent or minimal punishments passed down serve as little deterrent, with monetary penalties often being lower than the value of the meat itself (Barnett, 2000). As suggested by Nasi et al. (2008), these shortcomings point to both ownership and management problems; the State issues regulations to manage the resources it owns, but it is incapable of enforcing its decisions. Laws that are not enforced undermine government authority and those that are only enforceable with great difficulty and cost possibly need to be revised.

6. Impacts of over-exploitation

6.1. Impacts on wildlife populations

Of the many known threats posed to tropical forest biodiversity, hunting is of the most extensive. This activity can and often does trigger a multitude of direct effects on the targeted populations, which in turn indirectly effects the functioning of the ecosystem, as well as the ability of the resource to continually support human livelihoods (Bennett & Robinson, 2000; Harrison, 2011; Nasi, Christophersen, & Belair, 2010). Table 2 collates some of the prevailing empirical data relating to the sustainability of bushmeat hunting in the tropics. From here, it can be seen that such hunting is generally unsustainable across large swathes of the world's moist forests (Table 2, column I). This can be the case even at sites where hunting is conducted on a subsistence basis, mainly because tropical forests simply do not support high numbers of wild animals. The percentage of species hunted unsustainably appears to exceed 50% at various forest sites, although it should be noted that some studies are somewhat dated and it can be difficult to draw firm conclusions when only a small number of species is considered. Nonetheless, in a basin-wide study evaluating 57 of the Congo's mammalian taxa, Fa et al. (2002) showed that at least 60% of these taxa were harvested unsustainably, including 93% of the assessed ungulates and 63% of the primates and carnivores. Where hunting does occur sustainably, this is mostly at sparsely-populated, remote locations or at those outside the influence of external markets (Table 2). There is also some evidence for a situation of 'post-depletion sustainability' in long-established or 'mature' bushmeat markets, which have already passed through the 'extinction filter'. Cowlishaw, Mendelson, and Rowcliffe (2005) reported on such a phenomenon in the mature urban markets of Takoradi (Ghana), indicating that after the disappearance of vulnerable taxa (slow reproducers), the remaining more robust species (faster reproducers, such as rodents and some antelope) could be harvested sustainably. This proposition was, however, refuted by Waite (2007), who suggested that harvests in this region are in fact unsustainable.

Hunting at levels above those considered to be sustainable for a given species can lead to local population declines and, when severe and prolonged, to subsequent extirpation (this situation may be complex due to, inter alia, source-sink dynamics, spatial heterogeneity or high dispersal — see Nasi et al., 2011 and references therein). Thus, apart from assessing sustainability via the comparison of estimated productivity and off-take rates, an alternative method is to monitor the fluctuations in population densities of target species (Table 2, column II). Once again, that data currently available suggest that mammal densities are typically lower in hunted areas than in non-hunted areas across the tropics; at least 40% lower at sites in the Central African Republic (CAR), DRC and Gabon (although this may be up to 100%), 90% in the Amazon basin and 75% in India (Table 2, column II). In a more recent study focused on the northern CAR, a 94% decline in large mammals was registered between 1978 and 2010, with elephant (*Loxodonta africana*), Reduncinae and topi (*Damaliscus lunatus*) being hardest hit (Bouché et al., 2012).

While generally indicative of large-scale declines and unsustainable use, the aforementioned observations should be further qualified, since not all species respond equally to hunting pressure. Some species appear exceptionally vulnerable, others seem relatively unaffected and a few taxa can even be locally advantaged by hunting as a result of their ecological adaptability and population biology (Cullen, Bodmer, & Valladares-Pádua, 2000; Isaac & Cowlishaw, 2004; Peres & Dolman, 2000; Peres & Palacios, 2007). The most profitable and preferred species to hunt are generally the large-bodied ones, since these deliver more meat per capture than smaller species (Redmond et al., 2006). However, large-bodied and long-lived species with low intrinsic rates of population increase and long generation times (e.g. elephants, primates, large carnivores, tapirs, buffalo and other large ungulates) are considerably more susceptible to intensive hunting pressure than smaller species with high intrinsic rates of population increase (e.g. rodents, small to medium-sized duikers and peccaries) (Jerozolimski & Peres, 2003; Nasi et al., 2008; Peres, 2000a). As a result, the larger animals are often removed first. At least 12 large vertebrate species have been extirpated from Vietnam's forests since 1975 (Bennett & Rao, 2002b), while 25 large mammal species appear to be heading in the same direction in India (Karanth, Nichols, Karanth, Hines, & Christensen, 2010). Most large mammal species in Kilum Ijim (Cameroon) have become locally extinct due to hunting within the last 50–60 years, including elephants, buffalo, chimpanzees, bushbuck, lions and leopards (Maisels, Keming, Kemei, & Toh, 2001). Primates, in particular, have suffered immense overexploitation, in part because cultural values place high value on their meat, but also because they are large, noisy and gregarious and thus can be easily detected and bagged at high numbers in a single hunting excursion (Nadakavukaren, 2011). Hunting has reduced primate populations by up to 90% in some areas of Bioko (Equatorial Guinea)

Table 2
The estimated sustainability and decline in population densities of mammals due to hunting.
Modified from Nasi et al. (2008), Nasi et al. (2011), and Wilkie et al. (2011)).

Country/region — site	Main reason for hunting	Column I: percentage of species hunted unsustainably[a] (number of species studied)	Column II: percentage by which densities of target species are lower in moderately to heavily hunted forests than in un-hunted forest	Reference
Africa				
Congo basin		60% (57)		Fa et al. (2002).
CAR — Mossapoula	Subsistence/trade	100% (4)	43.9%	Noss (2000).
Cameroon	Subsistence/trade	100% (2)		Fimbel, Curran, and Usongo (2000).
Cameroon	Subsistence/trade	50–100% (6)		Delvingt, Dethier, Auzel, and Jeanmart (2001).
DRC — Ituri I	Subsistence		42.1%	Hart (2000).
DRC — Ituri II	Subsistence		12.9%	Hart (2000).
Gabon — Makokou			43–100%	Lahm (2001).
Eq. Guinea — Bioko	Subsistence/trade	30.7% (16)		Fa (2000).
Eq. Guinea — Rio Muni	Trade	36% (14)		Fa and Garcia Yuste (2001).
Eq. Guinea — Rio Muni	Trade	12% (17)		Fa, Juste, Perez del Val, and Castroviejo (1995).
Ghana	Trade	47% (15)		Cowlishaw et al. (2004).
Kenya	Subsistence/trade	42.9% (7)		FitzGibbon, Mogaka, and Fanshawe (2000).
Madagascar — Makira Forest	Subsistence	100% (5)		Golden (2009).
Latin America				
Brazil — 101 Amazon sites	Subsistence		90%	Peres (2000b); Peres and Palacios (2007).
Brazil — Mata de Planalto			27–69%	Cullen et al. (2000).
Bolivia	Subsistence	50% (10)		Townsend (2000).
Ecuador — Quehueiri-ono	Subsistence	30% (10)	35.3%	Mena, Stallings, Regalado, and Cueva (2000).
Paraguay — Mbaracayu	Subsistence	0% (7)	53%	Hill and Padwe (2000).
Paraguay — Mbaracayu	Subsistence		0–40%	Hill, McMillan, and Farina (2003).
Peru — Manu National Park	Subsistence	26% (19)		Ohl-Schacherer et al. (2007).
South/Southeast Asia				
Indonesia — Sulawesi	Subsistence/trade	66.7% (6)		O'Brien and Kinnaird (2000).
Indonesia — Sulawesi	Subsistence/trade	74% (4)		Lee (2000).
India — Nagarahole			75%	Madhusudan and Karanth (2000).

Abbreviations: CAR = Central African Republic; DRC = Democratic Republic of Congo; Eq. Guinea = Equatorial Guinea.
[a] Sustainability indicators reported here are generally determined through the examination of the relationship between estimated productivity and off-take rates.

(Fa, Yuste, & Castelo, 2000), while also being the main cause for the 50% decline in ape populations in Gabon over just two decades (Walsh et al., 2003). Likewise, hunted populations of spider (*Ateles* spp.) and woolly monkeys (*Lagothrix* spp.) in the Amazon basin have plummeted precipitously (Peres & Palacios, 2007).

Notwithstanding the countless species under threat by hunting, it should simultaneously be noted that many tropical forest and savanna landscapes carry a variety of species that continue to thrive in natural and modified habitats. In particular, rodents such as cane rats (*T. swinderianus*) and porcupines (*H. cristata*/*H. africaeaustralis*) are amongst the most abundant and resilient species hunted specifically for bushmeat in Africa (Bennett et al., 2007; Cowlishaw et al., 2005; Okiwelu, Akpan-Nnah, Noutcha, & Njoku, 2010). In addition, even in areas where larger species have been significantly reduced, some small and medium-sized ungulates can remain fairly unaffected or even increase in abundance (Nasi et al., 2011), probably due to the process of density compensation (see Peres & Dolman, 2000). In Gabon for instance, the small blue duiker (*Philantomba monticola*) is more abundant in hunted areas close to the town of Makokou than in the remote forests within the Ivindo National Park, whereas the larger Peter's (*Cephalophus callipygus*) and bay duiker (*Cephalophus dorsalis*) are less abundant or even depleted in the hunted areas (Van Vliet, 2008; Van Vliet et al., 2007). In the Amazon, peccaries are hunted sustainably more often than tapirs, even though the former make up a larger proportion of the off-take in terms of numbers and biomass (Swamy & Pinedo-Vasquez, 2014). Where declines of white-lipped peccaries (*T. pecari*) have been observed, these have been accompanied by increases in the populations of collared peccaries (*P. tajacu*) (Fragoso, 1994). The aforementioned examples suggest that the situation may not be dire for all species, however, it is clear that resource depletion and an overall lack of sustainability exist in many areas.

6.2. Impacts on ecosystems

With the persistent loss of larger-bodied species, forests can inevitably reach the point where the trees are standing but the fauna is not present — a phenomenon coined as 'empty forest syndrome' (Redford, 1992). Such a situation is symptomatic of large-scale overhunting and is being observed in many parts of the tropics (Corlett, 2007; Fa & Brown, 2009; Fa et al., 2002). More recently, 'empty savanna syndrome' has also become a reality as the commercial hunting for bushmeat continues to escalate in several African savanna habitats, draining vast wildernesses of their wildlife (Lindsey et al., 2013; Redmond et al., 2006). Even before this point is reached, however, there is considerable potential for ecosystem disruption and for cascading effects on the entire food web (Abernethy et al., 2013; Wright, 2003). Ecosystem processes are generally driven by the combined activities of many different species. While one depleted species might be replaced by another that fulfils a similar ecosystem function, not all species or functional groups are equally replaceable (Naeem et al., 1999; Nasi et al., 2010). 'Keystone species' or 'ecosystem engineers' are those species that have a disproportionately large effect on the environment relative to their abundance (Mills, Soulé, & Doak, 1993; Paine, 1966, 1969). Yet hunters frequently target larger-bodied animals, with many of these being keystone species, the loss of which can trigger dramatic impacts on ecosystems (Peres & Palacios, 2007; Stoner, Riba-Hernández, Vulinec, & Lambert, 2007; Terborgh, 2013; Wright et al., 2007). Local declines in top predators, for instance, can manifest in trophic cascades (i.e. changes in predator–prey relationships), altering the diversity and biomass of species across multiple trophic levels and leading to large regime shifts (Andresen & Laurance, 2007; Sergio et al., 2008; Terborgh & Estes, 2010; Terborgh et al., 2001). Elephants and other megaherbivores, on the other hand, play a central role in modifying vegetation composition and structure, including forest succession and regeneration patterns

(Babweteera, Savill, & Brown, 2007; Beaune, Fruth, Bollache, Hohmann, & Bretagnolle, 2013; Blake, Deem, Mossimbo, Maisels, & Walsh, 2009; Campos-Arceiz & Blake, 2011). Large-bodied frugivores (e.g. duikers, peccaries, primates and wild pigs) serve as the key seed dispersal agents for many plants, with reductions in their densities carrying major consequences for seed survival and forest regeneration (Beck, 2005; Bodmer, 1991; Nuñez-Iturri & Howe, 2007). Furthermore, primates can enhance the availability of accessible forms of nitrogen to plants, accelerate nutrient cycling and assist with the movement of nitrogen from fertile floodplain forests to nutrient-poor upland forests (Swamy & Pinedo-Vasquez, 2014). Moreover, these species need not be entirely extirpated from an ecosystem before significant functionality is lost. In the case of 'half-empty forests', species may still be present in a community, but they are sufficiently reduced to be considered 'ecologically extinct' and therefore no longer interact significantly with other species (McConkey & Drake, 2006; Redford & Feinsinger, 2001).

6.3. Impacts on human livelihoods

Returning back to the definition of food security (Fig. 2), it is clear that availability is a critical criterion for achieving food security, yet access must be sustainable in the long term. An individual or household cannot possibly be considered food secure if they have current access to adequate food to meet their immediate needs, while the natural capital that would provide for future needs is simultaneously being depleted (Sunderland, 2011). The sustainability dimension is thus an imperative component of the stability pillar, but is often neglected in the rush for short-term solutions (Poppy, Jepson, Pickett, & Birkett, 2014), potentially leading to a 'tragedy of the commons' situation (see Hardin, 1968). Failure to address the environmental and natural resource impacts will almost certainly hamper food supply, and thus also food security.

Given the scale and ubiquity of the current bushmeat harvest, it appears almost inevitable that wildlife collapses will continue unabated into the future, affecting the lives of many people (Swamy & Pinedo-Vasquez, 2014; Wilkie et al., 2011). Urban dwellers consuming bushmeat as a luxury item are unlikely to suffer nutritional hardship as a result of this forfeiture, since they can generally switch to other readily-available protein sources (Bennett, 2002). The tragedy, however, is that the direct costs of biodiversity loss are expected to fall heavily and disproportionately on millions of rural people across the developing world, who have very few affordable alternatives at their disposal (Milner-Gulland & Bennett, 2003). Despite the widespread reliance on bushmeat, surprisingly little research has been conducted to quantify the impacts of wildlife depletions on human health and livelihoods. Nevertheless, two seminal studies (Fa et al., 2003; Golden et al., 2011) have indicated that the loss of access to wildlife – whether due to strict enforcement of existing conservation policies or due to unbridled unsustainable harvests – will have direct and catastrophic effects on food security, nutrition and well-being, most markedly through waning supplies of crucial protein and micronutrients. Conservation policy enforcement would induce a more abrupt restriction of resources, whereas self-depletion would likely culminate, albeit more slowly, in irreversible local wildlife extirpations and obliteration of the harvested resource (Golden et al., 2011).

At present, a state of total food insecurity in the Congo basin is largely buffered by the availability of bushmeat protein (Fa et al., 2003). The reliance on bushmeat is emphasised by the fact that agricultural production is either declining or not increasing significantly in all Congo basin countries, apart for the CAR (Fa et al., 2003; Tollens, 2010). Nevertheless, bushmeat off-take levels in the region are ca. 50% higher than production and at least 4-fold higher than sustainable rates (Fa et al., 2002). Based on these extraction rates, bushmeat supplies from all Congo basin countries are predicted to drop by 81% by 2050 (Fa et al., 2003). In such a case, only three countries (Gabon, Cameroon and CAR) are likely to maintain their population's protein supply above the recommended daily requirement (ca. 50 g protein per day). Conversely, if sustainable harvests were to be enforced, all Congo basin countries would be dramatically impacted by the loss of bushmeat protein, except for Gabon, where the main source of non-bushmeat protein supply is imported. These findings not only indicate that a substantial number of forest mammals will become extinct relatively soon, but that protein malnutrition will increase radically in the region unless food security is promptly resolved (Fa et al., 2003).

Furthermore, a recent study conducted in rural Madagascar showed that the consumption of more bushmeat by children (<12 years of age) was associated with significantly higher haemoglobin concentrations (ca. 0.69 g/L) (Golden et al., 2011). It was predicted, however, that the loss of access to wildlife resources would result in a 29% increase in the prevalence of childhood anaemia, with a tripling of anaemia rates amongst those children in the poorest household (Golden et al., 2011). Anaemia, in turn, is known to progress to various other illness states, including cognitive, motor and physical defects. Thus, while numerous studies suggest that bushmeat provides a food security 'safety net' (Brashares et al., 2011; de Merode et al., 2004), Golden et al. (2011) reveal quantitative links between the micronutrients provided by bushmeat and crucial human health outcomes.

It is clear from the latter studies that bushmeat overexploitation represents a crisis from both a conservation and food security perspective. Nonetheless, the impacts on other human livelihood aspects should not be overlooked. At present, a widespread disruption of the bushmeat harvest could potentially affect just as many people in terms of income than in terms of diet, eroding one of the very few commodities that they have available to sell (de Merode et al., 2004; Milner-Gulland & Bennett, 2003; Swamy & Pinedo-Vasquez, 2014). While the trade in wildlife products is obviously a serious sustainability issue with cross-cutting implications, there is a clear need to separate out the profit-driven interests of those who capitalise on what they know to be an illegal activity with high commercial value (i.e. trade in rhino horn, tiger bone, pangolin scales) from the everyday means of survival of the poor (i.e. the large majority of the African bushmeat trade). A lack of sustainability of the harvest, more stringent controls or the blanket criminalisation of the trade will likely have dire impacts on the livelihoods of the latter group, potentially plunging them even deeper into poverty (Nasi et al., 2008).

7. Potential interventions and their challenges

It is almost 30 years since the alarm bells were first raised on the bushmeat crisis, as the impacts of the booming trade became increasingly known (Ntiamoa-Baidu, 1987). During these three decades, we have seen bushmeat escalate from a fringe concern of a handful of NGOs to an issue placed firmly on the international agenda (Redmond et al., 2006). Nonetheless, as the conflicting concerns and ethical arguments of conservation organisations and human development agencies continue to pull in different directions, we are left with very few innovative solutions to resolve the current problem.

The strict nature-preservationist response to the crisis has traditionally favoured prohibitive policies aimed at separating people and wildlife, such as expanding tightly-managed protected area networks, erecting higher fences and increasing enforcement and interdiction efforts (Lindsey et al., 2013; Minteer, 2013; Robinson, 2011). 'Fortress conservation' approaches may be useful to some extent, but their reach is generally limited since they address the symptoms of the problem and not the underlying causes (Rentsch & Damon, 2013). In the process, they tend to exacerbate poverty, forcing human displacement and loss of access to wildlife resources, with little or no compensation (Robinson, 2011; Roe & Elliott, 2006). The fact that the poorest people pay the highest price for such restrictions and for the concomitant loss of wildlife access is both an ethical and socio-economic issue, raising the question: is it ethically acceptable that the lives of the poor become even more impoverished? Of course, this is not the only ethical question that arises in the bushmeat debate, as the treatment of other species is also an ethical issue. Nevertheless, it could be argued that while the sustainable use of wildlife is ethically acceptable when this is necessary for human survival, when unsustainable use is driven solely by the short-term benefits of urban elites with alternative incomes, this becomes unethical (Williamson, 2002). Indeed, many conservationists contend that curbing the urban demand is the most logical solution to the current crisis (Robinson, Redford, & Bennett, 1999). It has further been suggested that, since much of the bushmeat consumed in urban households is supplied through logging concessions, increasing certification and preventing the hunting and export of bushmeat from these concessions could assist with reducing urban demand (Nasi et al., 2011).

Poverty alleviation has become the clarion call of the human development sector, based on the notion that this will effectively reduce the exploitation of wildlife resources (Robinson & Bennett, 2002; Swamy & Pinedo-Vasquez, 2014). Yet, the degree to which international development assistance caters for the needs of the rural poor is debated and its role in alleviating poverty will depend on how the aid is allocated and who benefits from it (Brown, 2007; Robinson & Bennett, 2002). Even if economic development is achieved, however, it cannot simply be assumed that this in itself will decrease bushmeat demand. Indeed, increasing wealth may increase this demand, as exemplified by the expanding urban market for bushmeat across parts of Asia and Africa (Brashares et al., 2011; Rentsch & Damon, 2013).

With top-down conservation approaches coming into question and social concerns gaining momentum, the last two decades have seen a proliferation of community-outreach programmes attempting to link biodiversity conservation within protected areas with socio-economic development outside of protected areas (Hackel, 1999; Wells & McShane, 2004). Widely referred to as integrated conservation and development projects (ICDPs), these approaches aim to provide incentives to local communities in exchange for curtailing illegal bushmeat hunting and trade, most often in the form of alternative livelihood opportunities, the provision of facilities (e.g. schools, clinics and roads) and shared decision-making authority (Barrett & Arcese, 1998; Newmark & Hough, 2000). Yet, in spite of their popularity and intuitive appeal, these proposed win–win approaches have suffered many practical failures, have generally faltered in achieving their desired outcomes and have been the target of considerable backlash (Agrawal & Gibson, 1999; Barrett & Arcese, 1995; Christensen, 2004; Gibson & Marks, 1995; McShane & Newby, 2004; McShane et al., 2011; Songorwa, Buhrs, & Hughey, 2000; Wells & McShane, 2004). The central stumbling blocks have included erroneous assumptions, poor planning, inadequate or short-term funding, the unilateral application of projects with little consideration of socio-economic factors driving overexploitation, the inability to provide real benefits at the household-level, as well as limited monitoring of outcomes and adaptive management strategies (Nyaki, Gray, Lepczyk, Skibins, & Rentsch, 2014; Roe & Elliott, 2006; Wicander & Coad, 2015).

Amongst the ICDPs, alternative income-generating strategies that have been promoted include livestock-rearing schemes, beekeeping, aquaculture and organic vegetable gardens (Wicander & Coad, 2015). Particularly favoured within this group has been the captive rearing of small, resilient wild species (e.g. cane rats, giant rats, porcupines, capybara and guinea pigs), since this could provide revenue while addressing local demand and preferences (Hoffman & Cawthorn, 2013). However, most bushmeat-rearing projects have had variable success, with the major obstacles being the high start-up costs, the difficulty in rearing certain forest species in captivity, the economic viability compared to domestic livestock rearing and the lack of donor support (Mockrin, Bennett, & La Bruna, 2005). Moreover, for alternative income-generating strategies to dissuade participation in the bushmeat trade, such opportunities need to compete with or surpass the earnings made through hunting (Tieguhong & Zwolinski, 2009). At comparable levels of profitability, hunting may still be preferred since it offers, inter alia, high returns on labour input and the ability to switch between consumption and trade (Van Vliet, 2011). Furthermore, given the limited conditionalities and sanctions associated with ICDPs, there is the added likelihood that the incomes generated through such initiatives would supplement rather than substitute those derived through bushmeat hunting and trading (Wicander & Coad, 2015).

Additional strategies to link conservation and development have taken the form of community-based natural resource management (CBNRM) programmes. Such approaches differ from other ICDPs in that, rather than offering development services in return for conservation, they devolve stewardship over wildlife resources to communities and generally allow management thereof through locally devised rules and procedures (Newmark & Hough, 2000; Roe, Nelson, & Sandbrook, 2009). The viability of CBNRM initiatives nevertheless relies on project communities seeing greater value in managing wildlife sustainably in the long-term compared to pursuing the short-term goals of illegal overexploitation. While not devoid of criticism, CBNRM has claimed some achievement in fostering compatible land-use regimes around protected areas in Zimbabwe, Zambia and Namibia (Newmark & Hough, 2000), as well as for conserving certain species in north-eastern Peru (Bodmer & Puertas, 2000).

Finally, game cropping operations have been conducted in certain community areas (including Zimbabwe's Guruve and Savé Valley Conservancy, and adjacent to Tanzania's Serengeti National Park) in attempts to provide villages with legally harvested bushmeat from well-managed or overabundant wildlife populations, with the assumption that this might create goodwill, increase the local valuation of wildlife and ultimately reduce illegal poaching (Holmern, Røskaft, Mbaruka, Mkama, & Muya, 2002; Le Bel, Gaidet, Mutake, Doze, & Nyamugure, 2004; Le Bel, Stansfield, La Grange, & Taylor, 2013). Nevertheless, projects that rely heavily on such wildlife harvesting have been criticised for being inefficient, uneconomical and potentially unsustainable, as well as for garnering limited levels of community involvement (Barrett & Arcese, 1998; Holmern et al., 2002; Nielsen, 2006). The cropping scheme outside the Serengeti, for instance, supplied legal meat from a modest 250–500 wildebeest per year, not nearly enough to deter the use of free, illegal bushmeat (Barrett & Arcese, 1998; Holmern et al., 2002). Moreover, this strategy is certainly not feasible under all scenarios. In Tanzania's Udzungwa Mountains, wildlife populations are too depleted to support cropping operations of any sort and it has been suggested that supporting efforts in this area be completely shifted to increasing the supply of domestic meat sources, rather than encouraging the use and dependence on wildlife through cropping programmes (Nielsen, 2006).

Finding substitute protein sources to avert bushmeat consumption has, however, posed a myriad of challenges. South America, with its thriving livestock industry, sets a prominent example of how developing diversified domestic meat sources can reduce reliance on bushmeat (Van Vliet, 2011). The flipside of the coin is that livestock ranching (e.g. cattle) is also a leading driver of deforestation in the region (Ilea, 2009). In many African countries, the expansion of the livestock sector may be comparatively less feasible, even apart from the frustrations of livestock disease, low animal productivity and meagre investments. A case in point is the Congo basin, where an area as large as 25 million hectares would need to be converted to pasture in order to replace the current bushmeat extraction (>4 million tonnes per annum) with locally-produced beef (Nasi et al., 2011). A focus on pigs and chickens, which have better feed conversion rates, faster growth rates and minimal space requirements, may represent a more achievable approach in the Congo basin countries. However, in the case that sufficient supplies of domestic protein were available, the potential for substitution will ultimately rest on price, taste and cultural preferences. Cheap domestic alternatives may well be embraced under some circumstances, but these will be exceptionally difficult to promote when bushmeat is cheaper (or free) or can be acquired at lower effort. In terms of the luxury urban market, where bushmeat is sought for its taste or cultural appeal and where ample domestic meat sources exist, this trade-off will be similarly improbable.

Alternative wild (non-bushmeat) protein sources, on the other hand, may well be considered appropriate substitutes. The importance of marine resources in the diets of tropical forest inhabitants is well known (Nasi et al., 2008), with fish and bushmeat often being exchanged for one another according to price and availability. Using 30 years of data from Ghana, Brashares et al. (2004) showed that people turn to bushmeat when fish yields are low, with such declines being expedited by EU-subsidised fleets operating in the region. There could thus be some hope for reducing bushmeat demand if this trend could be reversed; however, such a proposition appears exceedingly unlikely given the ever-worsening state of world's fish stocks (FAO, 2014b; Inogwabini, 2014). The other potential wild alternative, invertebrates (e.g. snails and caterpillars), can be locally important dietary items, but their general seasonality makes them unlikely candidates to fully replace bushmeat (Van Vliet, 2011).

Given the multiple constraints on supplying alternatives and prohibiting off-takes, there is now growing consensus that achieving sustainable bushmeat harvests is by far the most pragmatic option for simultaneously promoting biodiversity conservation, food security and local livelihoods (Nasi et al., 2011). In spite of its appeal to doctrinaire conservationists, there is also increasing realisation that a blanket ban on bushmeat hunting, when applied outside of protected areas, is not the most realistic or effective strategy to address the problem (Bennett et al., 2007; Brown, 2007; Nasi et al., 2008). Such a proposition is echoed by Egbe (2000), who suggests that “a law which makes the most common form of conduct illegal is itself an instrument of indiscipline and serves neither the interests of the State nor the communities”. Some of the species targeted in the bushmeat trade, such as rodents, blue duiker (*P. monticola*) and collared peccaries (*P. tajacu*), reproduce rapidly and are more resilient to overexploitation (Bennett et al., 2007; Nasi et al., 2008). Bringing the trade of such species into the formal economy (while maintaining restrictions on vulnerable species), might provide the impetus required to effectively monitor and manage the stocks (Rowcliffe, Milner-Gulland, & Cowlishaw, 2005).

8. Conclusions

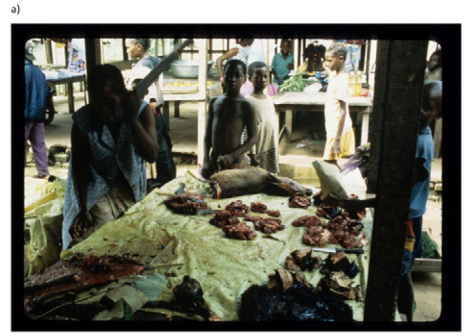
Whether its activities are legal or illegal, the bushmeat problem raises an intricate complex of environmental, economic, social, cultural and ethical challenges. Any solutions proffered to mitigate its impacts must reflect this, being amendable to various compromises and concessions to achieve a realistic and balanced policy response. Approaches that focus narrowly on biodiversity conservation, when articulated at the expense of human health and livelihoods, are unlikely to be sustainable in the long term. However, the combination of environmental and social perspectives aimed at understanding how wildlife and people are interlinked, as well as the mechanisms that strengthen or weaken these linkages, will likely make the end goal considerably more achievable. In the words of biodiversity scientist John Robinson (2011): “ultimately conservation approaches must be sustainable – ecologically, culturally, socially, economically and politically – otherwise they will fail both practically and ethically”.

Addendum 1

Fig. A. Locals smoking elephant in Cameroon.
Source: Andre de Georges.

Fig. B. Mice being sold on the roadside.
Source: Andre de Georges.

a)



(b)

Fig. C. Fresh (a) and smoked (b) duiker being sold in bushmeat markets.
Source: Andre de Georges.

(a)
(b)
(c)


Fig. D. Monkeys being caught (a, b) and smoked (c) in Cameroon. Source: Andre de Georges.

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