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Bushmeat harvest in tropical forests

Knowledge base, gaps and research priorities

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CIFOR

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Photo by Ollivier Girard/CIFOR
Jeanne Mwakembe at the Moutuka Nunene market in Lukolela, Democratic Republic of Congo.

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1 Introduction

For millennia, terrestrial wildlife has been the primary source of protein and a major contributor to local livelihoods for millions of tropical forest inhabitants worldwide. Although humans have always used wildlife as a source of food and materials, the scale of the current harvest is unprecedented and is growing rapidly. Increasing demand for bushmeat and animal-based products, development and dissemination of modern firearms and other more effective methods of hunting, and increased access to remote forests, have combined to create an unprecedented pressure on wild animal populations in tropical forests worldwide (Robinson and Bodmer 1999).

To date, much research effort has focused on documenting and measuring the impact of bushmeat harvest on populations of targeted game species. This has resulted in conservation efforts being focused on the protection of these species and the criminalization of bushmeat harvest in many regions as part of conservation policies, often in areas that were formerly traditional hunting grounds. In contrast, the premise that bushmeat is an important resource provided by forest ecosystems is not well accepted and relatively little research has been undertaken to devise strategies for the management and sustainable use of bushmeat. Furthermore, research on bushmeat harvest is unevenly distributed, thematically and institutionally, across the three main regions of tropical forest – the Neotropics, Afrotropics and Asian tropics. Much of the existing data is not open-access, and is owned by individual researchers and private conservation groups. Given the current fragmented understanding of bushmeat harvest, there is limited technical-scientific information on the relationship between game species and the provisioning of ecosystem services and the capacity of bushmeat to enhance or constrain adaptive responses to ongoing socio-environmental change (e.g. climate change, urbanization, land-use change, etc.). These issues are crucial for any effort to ensure human well-being and environmental conservation in tropical forests.

This paper aims to shift the focus of current and future research efforts on bushmeat harvest towards the issue of sustainability, which must include ecosystem function and livelihoods, and game populations. Section 2 examines the current state of knowledge of bushmeat harvest in tropical forests, focusing on three key thematic areas: the impact of bushmeat harvest on target game populations; the contribution of bushmeat harvest towards the livelihoods of more than one billion people; and the effects of bushmeat harvest on ecosystem processes and services that contribute to forest maintenance. Section 3 examines some of the key drivers of bushmeat overexploitation in tropical forests. Section 4 provides a brief overview of past attempts, and current and future opportunities for efforts to improve the sustainability of bushmeat harvest through management and intervention. Section 5 presents a concise summary of current knowledge gaps and highlights the needs and opportunities for critical research, directed at two key issues: How can existing research information be used and synthesized to improve the sustainability of bushmeat harvest? What additional information and research will be useful to further ensure the long-term sustainability of bushmeat harvest? Ongoing and future research efforts that focus on these issues will greatly help stakeholders and policy makers in making informed decisions aimed at the sustainable procurement of bushmeat, and the management and conservation of game species and their habitats.

2 Bushmeat harvest research: Knowledge base

2.1 Game populations

2.1.1 Global and regional scenarios

Bushmeat harvest has a profound impact on hunted species globally. Although non-threatened species are hunted more frequently than threatened ones (Nasi et al. 2011), hunting is a primary threat to about 85% of the primates and ungulates that are endangered or critically endangered according to the IUCN Red List (Table 1). Over 93% of endangered, large-bodied, ground-feeding birds (Galliformes – pheasants, fowls, guans, curassows, etc.) are threatened mainly by hunting (Table 1).

The impact of hunting varies among tropical continents. Globally, many species are being hunted at an unsustainable level, which has already led to increases in prices and shifts toward less desirable species. Large game species are more vulnerable in tropical forests since these ecosystems are less productive overall than savannahs or grasslands (Bennett and Rao 2002). Most of the data and all of the synthetic analyses of bushmeat harvest come from Central and Western Africa or the Neotropics, especially the lowlands of Brazil and eastern Peru, although recent years have seen more systematic approaches to research elsewhere, such as in India (Velho et al. 2010) and Indonesia (Lee et al. 2005). It is estimated that 150,000 people in forest ecosystems of the Neotropics and 4.9 million people in the Afrotropics consume a total of about 5 million tons of wild mammal meat every year (Fa et al. 2002), and more recent estimates suggest that the total is closer to 6 million tons (Nasi et al. 2011). The evidence suggests that it is impossible to sustain the current levels of hunting in the long term (Wilkie et al. 2011) and the eventual collapse of game populations will reduce the availability of food and income to the people who currently rely on them. Models examining the risk to hunted animals from all sources, including random events such as weather anomalies, in addition to steady hunting pressure, predict that future populations of bushmeat species will sometimes show gradual declines, but will also experience abrupt population crashes (Barnes 2002).

Hunting in fallows is an important source of food and income for low-income families that are experiencing accelerated processes of deforestation

Table 1. Endangered animals and hunting pressure (IUCN 2012).

	Endangered and critically endangered species	Number with hunting as a primary threat	
All mammals:	642	297	46.3%
Primates	108	127	85.0%
Ungulates	50	59	84.7%
Lagomorphs	7	13	53.8%
Rodents	41	211	19.4%
All birds:	586	230	39.2%
Galliformes	29	27	93.1%
Ducks	14	14	82.5%
Pigeons	24	19	79.2%

and fragmentation. As mature tropical forests outside protected areas are rapidly vanishing, local people are increasingly dependent on fallows as hunting grounds. Data from secondary forests, fallows, fields, and other matrix habitats suggest that these areas could play an important role in providing bushmeat from less-threatened species (Robinson and Bennett 2004). However, research to date has been limited and the knowledge base is sparse compared to our understanding of forest dynamics in both the Neotropics and Afrotropics.

Comparative studies on hunting pressure in the Amazon and Congo have reported that, while no Amazonian mammals were exploited unsustainably, 60% of the mammals in the Congo were, according to the Robinson Redford index (Fa et al. 2002). Other studies of offtake by indigenous groups in the Amazon have shown that their harvest of bushmeat depleted species only at a very local level (Ohl-Schacherer et al. 2007). However, the index values should not be interpreted to mean that the Amazon is hardly affected by hunting; the biomass of the 12 most harvest-sensitive species in the Amazon is reduced more than 90% from 979.8 kg/km^2 to only 89.2 kg/km^2 in heavily hunted sites (Peres and Palacios 2007), with profound effects on ecosystem function.

With the exception of China and India, historical records of faunal changes in Asia are sparse and specific reports are scattered, but regional declines in most species have occurred largely within the last 50 years (Corlett 2007). In India, a recent study estimated that 25 large mammal species showed substantial probabilities of local extinction over the past century (Karanth et al. 2010). Although limited research effort has focused on rigorously quantifying hunting pressure in India (Velho et al. 2012), even the sparse available information suggests strong historical pressure on wildlife populations. For example, a report from Arunachal Pradesh, a state with considerable forest cover and extent, concluded that 20 of the 33 mammals hunted there are endangered, vulnerable or near threatened according to the IUCN Red List (Aiyadurai et al. 2010). A study that examined the trade in babirusas and wild pigs in North Sulawesi, Indonesia, found that dealers drove significantly farther to buy wild pigs, paid more for them and bought fewer in 1997 than 10 years earlier (Milner-Gulland and Clayton 2002). Such examples have not been compiled on a wide enough scale to yield synthetic statements about the region, as has been done for the Neotropics and Afrotropics, but there is ample documentation of local effects. Overall, the commercial wildlife trade is vast, and mainly supplies an urban luxury market for meat and traditional medicine (Bennett and Rao 2002). Urban markets and the trade in animal parts for medicines, raw materials and pets have grown markedly over the past 50 years, outstripping the intensification of subsistence hunting (Corlett 2007).

Whether and under what circumstances bushmeat harvest is sustainable is a controversial issue, often pitting conservation biologists against those who emphasize the benefits that bushmeat provides to humans. Such debates tend to be on a policy level, but sometimes, different researchers draw conflicting conclusions even from the same regions and data sets. For instance, one group of researchers (Cowlishaw et al. 2005) suggested that West African bushmeat markets have shifted to robust taxa that can withstand high hunting pressure and provide a sustainable source of bushmeat. However, their methodologies came under criticism by another researcher (Waite 2007), who argued than the harvest of those species was unsustainable. In many cases, the authors who discuss these issues fail to distinguish between the different types of hunting: local hunters, who are primarily hunting for subsistence versus immigrant hunters, who harvest bushmeat for urban markets. However, changes in market demand also change the dynamic – local hunters are increasingly hunting for the market as society is becoming more urban in most countries.

2.1.2 Game species characteristics

The species that are most popular with hunters tend to have large body size (Peres 2000), a feature associated with a suite of life-history traits that make these species more easily subject to overexploitation, including low reproductive rates, low population densities, long generation times and long life-spans (Jerozolimski and Perez 2003; Isaac and Cowlishaw 2004). Hunting tends to remove large-bodied wildlife first (Jerozolimski and Perez 2003), and larger animals decline faster in over-hunted sites (Peres and Palacios 2007). Once the larger animals are removed, medium-

sized species (between 2 and 50 kg) are the most frequently hunted, e.g. in the Amazon and the Congo Basin, though larger species are taken when possible (Nasi et al. 2011). In both basins, primates are commonly hunted, but because of their small body size, they do not make up a great proportion of the offtake biomass. Instead, large rodents and ungulates, especially duikers in Africa and peccaries in the Amazon, represent the bulk of the biomass.

Specifically, in a large-scale study of bushmeat markets, mammals represented more than 90% of the meat sold from central African moist forests; reptiles are common, but birds and amphibians are scarce (Fa et al. 2009). Among those mammals, most were ungulates (36–40%) and rodents (34–38%), with primates representing fewer (13–19%) carcasses (Jerozolimski and Peres 2003). Bushmeat markets in the Amazon are heavily dominated by peccaries and paca, which in one study represented 36.9% and 28.4% of records and 47.9% and 20.6% of biomass, respectively (Suarez et al. 2009). More specific information on the hunted populations are beyond the scope of this report, but their status assessments are synthesized elsewhere for key animals of the African rain forest (Bakarr et al. 2001) and the Amazon (Peres and Palacios 2007).

Data on bushmeat markets from tropical countries reflect local conditions such as the decline of local populations and in some cases the extirpation of large mammals. In North Sulawesi, Indonesia 96,586 wild mammals were recorded during market surveys. Most were small-bodied rodents, which accounted for 43.9% of all encounters, followed by large bats (39.8%), small bats (7.5%), and Sulawesi pigs (7.3%) (Lee et al. 2005).

In addition to body size and taxonomic affinities, an animal's guild may affect its persistence in hunting areas. In the Amazon, frugivorous species showed more marked declines in abundance in heavily hunted sites than did seed predators and browsers, regardless of body size (Peres and Palacios 2007). Finally, certain behavioral traits that are found across taxa make some animals more likely to be hunted than others. If the species has ostentatious mating behaviors that attract attention, or congregates in high densities to nest or feed, it is more likely to be hunted (Wilkie et al. 2011).

From an ecological standpoint, the animals that are most often hunted may not be those that are the most sensitive to hunting. In the Amazon, for instance, peccaries are sustainably hunted more often than tapir, though they represent more of the take in terms of numbers and biomass (Aquino et al. 2008). Neotropical primates usually represent a much smaller proportion of hunted biomass than ungulates, but they are very sensitive to hunting pressure (Table 2) and often are over-hunted (Aquino et al. 2008). Similarly, galliform birds are comparatively rare in bushmeat markets, but globally, the group is highly threatened by direct pressure from hunting (Keane et al. 2005).

One limitation of many of the studies of bushmeat populations is the tendency for field studies to focus on one or only a few species. Offtake estimates based on research in markets usually

Table 2. Amazonian vertebrates species whose populations are most threaten (Peres and Palacios 2007).

Latin name	Common name	% reduction in abundance
Cacajao calvus	Uakari monkey	90–97
Langothrix lagothricha	Woolly monkey	68.5–90
Geochelone denticulata	Amazonian tortoise	
Aburria jacutinga	Guans	
Ateles belzebuth	Spider monkey	
Tayassu peccari	White-lipped peccary	
Callithrix jacchus	Marmosets	~68.5
Callicebus torquatus	Collared titi monkey	
Mitu mitu	Curassows	
Tapirus terrestris	South American tapir	
Cebus paella	Tufted capuchin monkey	

document all wild species that are for sale, but fieldwork and estimates based on wildlife censuses usually focus on fewer or a single species; the most common index of sustainability is based on a single species (Robinson and Redford 1991). To better understand the effects of hunting, research must consider wider selections of prey, which will vary according to the fluctuations of availability and the market. Some researchers have begun to consider multiple species of prey using modeling techniques (Rowcliffe et al. 2003), but in general, the interspecific dynamics of hunting are poorly understood.

2.1.3 Hunter characteristics

Hunters can be either from the area where the animals are harvested, or immigrants that are brought there by economic opportunities such as logging or oil exploration (Suarez et al. 2009). For instance, in Sarawak, Bennett found that bushmeat was present in 29% of meals in the interior, but in 49% of meals in logging camps (Bennett et al. 2007). A second important distinction is whether hunters transport game meat for sale in markets or cities, or use the meat for their families and near neighbors. Urban hunters from low-income families are believed to be the main suppliers of bushmeat in the growing urban markets in the Amazon.

Although the consumption by people living near the forest may be sustainable, the demand for bushmeat among more affluent people in urban areas may drive harvest levels that are too high to maintain healthy populations of the hunted animals (Wilkie and Carpenter 1999). In the Democratic Republic of Congo (DRC), for example, large and protected species, such as elephant and buffalo, are rare in rural markets, but represent more than half of bushmeat sales in cities, especially during times of civil unrest (de Merode and Cowlishaw 2006). Another study in northern regions of the DRC found that 72% of the bushmeat harvest was carried out by immigrants to the area (Poulsen et al. 2009). Unsustainable hunting is also reported to take place in regions that are under conflict and where bushmeat is the main source of protein for armies.

In the Amazon, hunters tend to extract large-bodied game from mature forests, more than from any other type of habitat, even though the capture rates per unit of hunter effort are relatively low (Gavin 2007; Parry et al. 2009). Research in the Amazon tends to be weighted toward indigenous hunters, and the urban demand for bushmeat is lower than in the Congo Basin. This underscores the need, mentioned above, for a better understanding of the capacity of secondary forests, fallows, and other unprotected, non-mature habitats (Robinson and Bennett 2004).

2.1.4 Measurement of harvesting impact

The most straightforward measure of the ecological impact of bushmeat harvest is the change in target animal populations. Research has taken different approaches toward quantifying these effects, from attempting to document the biomass of species, to using sophisticated models to account for variations in hunting pressures (Wiederholt et al. 2010). Many studies rely heavily on information from interviews with hunters and on the availability and price of bushmeat in markets, especially in Africa (e.g. Fa et al. 2004; Dupain et al. 2012), and some studies measure the abundance of the target populations, although this approach is more common in the Neotropics (e.g. Peres and Palacios 2007). The Robinson and Redford index of sustainability (Robinson and Redford 1991) is by far the most common metric to evaluate the exploitation of a single species. It calculates the maximum potential production of a species from the population carrying capacity and the intrinsic rate of increase. Although its popularity allows for comparisons among locations and species, this approach has been criticized as over-simplified and for failing to incorporate potential changes in human behavior (Ling and Milner-Gulland 2006). Advances in ecological modeling should make it possible to refine this and related indices to give a more reliable account of harvest. The biomass of extracted species is also a common metric and offers a multispecies assessment. Biomass measures are more ecologically relevant because large vertebrates that are favored by hunters are a dominant component of animal biomass in unhunted tropical forests and have disproportionately important roles in regeneration processes and ecosystem functioning (Redford 1992; Terborgh et al. 2008).

2.2 Livelihoods

Although bushmeat harvest may not be sustainable at current levels of exploitation, it provides many benefits to the human populations that use these resources. Bushmeat provides protein in places where protein is scarce and important. Furthermore, its trade is easy to enter, low risk and seasonally flexible, making it particularly attractive to rural populations. In comparison with forest products such as timber, a higher percentage of the income from bushmeat remains in the hands of the primary producer (Brown 2003).

2.2.1 Nutritional dependency

From 1990 to 2009, the number of undernourished people in the developing world fell both in prevalence (from 23.2% to 15.5%) and in absolute numbers (from 1 billion to 852 million).[1] Nevertheless, there are 868 million undernourished people in the world today (Estes et al. 2011), and there is a striking overlap between countries with higher numbers of poor and hungry people and countries with a higher biodiversity (Mainka and Trivedi 2002). The importance of bushmeat to the nutrition of the people who consume it has been the object of many studies. To some communities, it is more important than any other source of protein (Fusari and Carpaneto 2006). Bushmeat can be one of the cheapest forms of protein, even in substantial urban markets where prices are lower than those of domestic meat, as is the case in the capital of Orientale Province in the DRC, a city of 680,000 people (van Vliet et al. 2012).

Rural hunters who eat bushmeat in the Amazon are estimated to consume 63 ± 25 kg/person/year and those in the Congo Basin consume 51 ± 14 kg/person/year. Consumption by urban people on the two continents, however, is very different, and bushmeat is not always important in providing protein or meeting basic needs. In the Congo Basin, which has a significant urban market, total bushmeat consumption can increase with income in some areas (Nasi et al. 2011). For instance, a survey in Brazzaville in 2006 revealed that 88.3% of the surveyed households consumed bushmeat, primarily because of its flavor and because of traditional food habits (Mbete et al. 2011). Food preference enhances the commodity chain where the very poor are more likely to benefit from the bushmeat trade than from consuming bushmeat (de Merode et al. 2004). Only 5 to 8 million people, or 1.4–2.2% of the population in South America rely regularly on bushmeat as a source of protein in their diets. Very few of those people are in cities, and they are likely to be some of the poorest in the region (Rushton et al. 2005).

There is a significant body of literature on the importance of bushmeat as a source of protein in various human populations, but only a few highlight the role of bushmeat in the basic nutrition of its consumers. A recent study (Golden et al. 2011) found that children in rural Madagascar who consumed more wildlife had higher hemoglobin concentrations, and that banning its consumption would increase childhood anemia rates by 29%.

2.2.2 Food security

Food security means having access to enough food at all times for an active and healthy life. Bushmeat contributes most to food security where it is the only or main source of animal protein (Mainka and Trivedi 2002), which applies to only part of the global bushmeat market. Bushmeat is used more heavily during certain seasons, or to supplement diet during difficult moments in the agricultural cycle. It is critical to human welfare in some cases, e.g. in Tanzanian refugee camps, where the refugees have almost no access to other sources of protein (Jambiya and Millendge 2007). Although the domestic use of bushmeat was once considered to be its most important use (Scoones et al. 1992), bushmeat contributes indirectly to food security by providing income from sales or distribution to outside markets (Mainka and Trivedi 2002; de Merode et al. 2004).

Better management of game populations will be required to maintain the current dependence on bushmeat, and will entail an immediate cost to people who rely on bushmeat or bushmeat harvest. At current exploitation rates in the Congo Basin, the bushmeat protein supply is projected to drop by 81% within 50 years. On the other hand, reducing current hunting levels to what is sustainable in the long-term would reduce access to protein and dramatically affect the people who currently rely on bushmeat (Fa et al. 2003).

1 http://www.fao.org/hunger/en

2.2.3 Income dependency and employment

At present, a global disruption of bushmeat harvest would affect more people in terms of income than diet, though the potential impact varies widely across continents and even within relatively small areas. Subsistence hunting is strongly linked to low income and low protein intake in some areas (Nielsen 2006), but the rapidly expanding luxury, urban and international markets have made commercial hunting more important than household hunting in many cases, e.g. for the hunting of apes in Africa (Miranda and Alencar 2007; Kuehl et al. 2009). Where bushmeat markets are growing, rural people are exploiting their wildlife resources to subsidize the protein consumption of urban families (Bennett et al. 2007). In one of the most comprehensive studies to date, using data from Cameroon, Ghana, Madagascar and Tanzania, Brashares et al. (2011) found that in rural settings the poorest households consistently consume more bushmeat, whereas bushmeat consumption is positively related to income in urban settings. The demand for bushmeat and its prices make it as important in terms of income for urban people as it is for the nutrition of the rural poor.

The empirical evidence for a significant role of bushmeat in household income in tropical rural communities is relatively limited, and so diverse as to defy a coherent summary (de Merode et al. 2004). One complicating factor is that the commodity chains are quite variable. At times they might include only a hunter and his neighbors, but they may also stretch through many rural hunters to traders along the major transportation routes, to roadside restaurants or to market-stall owners, and finally to urban consumers (Bowen-Jones et al. 2003). In Zimbabwe, bushmeat hunting is conducted mainly by unemployed young men to generate cash income, which is then used to purchase other food supplies (Lindsey et al. 2011). In Gabon, bushmeat was hunted less by the poorest families, but after a certain threshold was reached, income and offtake were not correlated (Coad et al. 2010), and most of the income difference was spent on luxury items such as alcohol and cigarettes. In their study of extremely poor households in the Democratic Republic of Congo, de Merode et al. (2004) found that although wild foods do not make up a significant portion of the regular household diet; they become important for household consumption during the four months of the lean season when the community is most vulnerable to food shortages. Throughout the year bushmeat was important to the community as a source of income. This basic pattern has also been documented in Equatorial Guinea (Kumpel et al. 2010).

As noted above, hunting in the Amazon tends to be more for subsistence and less for sale than hunting in Africa, so the Amazonian bushmeat trade is more often related to nutritional dependence than to income dependence. However, the comparison is relative, and income dependence also exists in the Neotropics. The annual bushmeat trade has been estimated to represent USD 1.13 million in Loreto Department, Peru, and reducing offtake to sustainable levels is likely to reduce that trade by 36.4%, with a profound impact on incomes in the rural sector (Bodmer and Lozano 2001). In general, bushmeat consumption increases with wealth in the Amazon, as traditional hunters acquire firearms (Godoy et al. 2010), but is not traded on the same scale that it is in Africa.

2.3 Ecosystem function

The harvest of bushmeat has effects that extend well beyond the direct impact on hunted species. Redford (1992) highlighted the "empty forest" phenomenon, i.e. forests that retain an intact adult tree community but are devoid of large vertebrates as a result of ecologically unsustainable rates of extraction through subsistence and/or commercial hunting. Plant–animal interactions are vital in sustaining tropical forest ecosystems and maintaining biodiversity, because animals play crucial roles at every step in plant reproduction and regeneration processes: pollination, seed dispersal, seed and seedling predation, and seedling growth and maturation (Terborgh et al. 2002). Consequently, any human-induced alteration of the faunal community within an ecosystem will disrupt the processes that control the regeneration of its plant community. Tropical forests are particularly vulnerable to such disruptions because of their high floral and faunal diversity, and because of the extent and complexity of plant–animal interactions in these ecosystems (Janzen 1970; Connell 1971).

Owing to the complexity of ecological interactions in the high-diversity forest ecosystems inhabited by many game animals, the full impact of defaunation on ecosystem processes and services is often difficult to characterize and may take decades to manifest. Most of the research to date has been done in the Neotropics, but there is compelling evidence from each continent that the loss of wildlife disrupts ecological and evolutionary processes, alters species compositions, and reduces biodiversity. Although specific pathways and mechanisms vary widely among the systems that have been examined (Stoner et al. 2007a), the accumulated evidence to date suggests that reforestation and restoration efforts may be in vain if the complementary fauna are not restored (Brodie and Aslan 2011).

The most significant indirect effects of bushmeat harvest are experienced by the plant community, which relies heavily on animals for pollination and seed dispersal in tropical forests. Over 150 animals serve to disperse the seeds of 75% of woody species in tropical forests (Muller-Landeau and Hardesty 2005). By ingesting mature fruits in the canopy or at the base of fruiting trees and later dispersing the seeds away from their parent trees, vertebrate frugivores are in effect ensuring the "escape in space" of these seeds through the avoidance of consumption or infestation by a variety of host-specific seed and seedling predators and pathogens that operate in areas of high seed and seedling density around reproductive trees (Janzen 1970; Connell 1971). Hunting can eliminate or greatly reduce the biomass of large-bodied frugivores (Peres and Palacios 2007), which invariably leads to a significant reduction in seed dispersal rates (Markl et al. 2012). Large-seeded plant species are most affected by the loss of dispersers, such that defaunated forests favor plants dispersed by non-hunted animals such as bats and small rodents, or by abiotic means such as wind or explosive dehiscence. This has been documented in tropical forests of Africa (Wang et al. 2007; Vanthomme et al. 2010), Asia (Sethi and Howe 2009), and the Neotropics (Wright et al. 2007; Nunez-Iturri et al. 2008;Terborgh et al. 2008). The overall effect of these processes on the forest is a shift in species (away from large-seeded trees that rely on animal seed dispersal), a reduction in species richness, and greater dominance by fewer species of plants.

Other taxa that can be affected by hunting are directly responsible for seed predation. Where large frugivores have been hunted out, small-seeded plants may suffer abnormally high seed predation from small rodents, while large-seeded species escape predation. In Los Tuxtlas, Mexico, this pattern is thought to have resulted in dense seedling carpets dominated by large- seeded species in the understory, and may explain the low seedling diversity in heavily hunted areas elsewhere (Dirzo et al. 2007). In fragmented landscapes, large fruit bats (Kamins et al. 2011) and pigeons are particularly important for seed dispersal, but they also face heavy hunting pressure, which reduces dispersal volume and distance (Corlett 2009). The community level alterations that result from hunting may affect ecosystem services and processes. For instance, the local extinction of some species of vertebrates has reduced the recruitment of some species of trees that are used by people as forest products (Forget and Jansen 2006). Defaunation may also affect ecological resilience in the face of climate change. Tree species are expected to adapt to climate change by shifting their distributions as climate conditions alter, but their capacity to do so will rely in large part on their dispersal ability (Clark et al. 2003; Zhu et al. 2012). Therefore, large-seeded, vertebrate-dispersed species are particularly vulnerable to climate change-induced range contraction in the absence of seed dispersal services provided by large vertebrates that are often highly harvested game species.

Large game animals, such as elephants in the Paleotropics, and tapirs and white-lipped peccaries in the Neotropics, are considered "ecosystem engineers" in terms of their ability to shape the vegetation in their habitats through their foraging habits and movements (Keuroghlian and Eaton 2009; Beck 2005; Fragoso 1997). Their absence can lead to alterations in seedling recruitment and understory vegetation structure (Queensborough et al. 2012). In addition, vertebrates can also play a role in nutrient cycling in tropical forests. In the Neotropics, primates increase the availability of accessible forms of nitrogen to plants, increase the speed of nutrient cycling (Feeley and Terborgh 2005), and move nitrogen from the fertile floodplain forests to upland forests that tend to be poor in nutrients (Stevenson and Guzmán-Caro 2010). Although these effects have been documented, the effects of defaunation on nutrient cycling remain poorly understood. Recent research has demonstrated that the depletion of game mammal populations by subsistence or

commercial hunting in tropical-forest systems can severely disrupt the diversity and abundance of dung beetle communities through alterations in the composition and availability of dung resources (Nichols et al. 2009). This, in turn, has significant short- and long-term implications for the maintenance of key ecosystem processes, including nutrient recycling and secondary seed dispersal.

Excessive levels of bushmeat harvest can have "trickle-up" as well as "trickle-down" effects. For example, top predators compete directly with hunters for the same species of prey, and their populations can decline as a result of hunting (Henschel et al. 2011). Predators structure vertebrate assemblages by decreasing the numbers of smaller predators and regulating prey populations. Local extinction of predators can also lead to trophic cascades, i.e. changes in predator–prey relationships that alter the biomass and diversity of species across multiple trophic levels (Terborgh et al. 2001; Wright 2003). A recent compilation of decades of research, conducted in a variety of terrestrial and aquatic ecosystems across the planet, reveals extensive cascading effects of the disappearance of large apex consumers on processes as diverse as the dynamics of disease, wildfire, carbon sequestration, invasive species, and biogeochemical cycles (Terborgh and Estes 2010). These findings emphasize the urgent need for interdisciplinary research to forecast the effects of trophic downgrading on processes, functions and resilience in global ecosystems (Estes et al. 2011).

3 Drivers of bushmeat over-exploitation

3.1 Demographic change, urban and international markets

Urban areas of the world are expected to generate most of the global population growth over the next four decades, partly by incorporating portions of the current rural population. Most of the urban population growth will be in cities in less developed regions. The urban populations of Asia, Africa and Latin America are projected to grow by 1.4 billion, 0.9 billion and 0.2 billion, respectively. The continuing increase in bushmeat supplies to urban markets, coupled with the projected growth in human population, suggest that these demographic shifts will be of enormous importance to the harvest of bushmeat in the coming decades.

As previously mentioned, demand is increasing for bushmeat as a luxury item in urban markets. Bushmeat can serve important cultural roles by indicating status or by maintaining cultural ties to rural family or ancestors. In Vietnam, for example, bushmeat is primarily consumed by successful, high-income earners (men) who wish to communicate their high status in society. This demand is only projected to increase in line with economic growth (Drury 2011). Urban markets have a profound effect on the species that are targeted by hunters. In Equatorial Guinea, where hunting for urban markets is an important contribution to many household incomes (Kumpel et al. 2010), villages that rely on traders target species with the greatest markup in price; villages with easy access to markets target other species that are more profitable for the hunter (Allebone-Webb et al. 2011). Such market forces are more important than other factors in determining the target species. Bushmeat markets follow the growth of other forest industries, such as oil extraction, that attract people to remote areas and increase connectivities (Suarez et al. 2009). Markets that persist often see a shift from the largest and most vulnerable species to smaller, more robust, and rapidly reproducing species, such as rodents (Cowlishaw et al. 2005).

The demand for bushmeat has also created an international market, though most international trade is more likely to be for medicinal or other purposes. Nevertheless, an estimated 5 tons of bushmeat is smuggled in personal baggage through Paris' Roissy Charles de Gaulle airport each week, most likely for clients who consume it as a luxury food item (Chaber et al. 2010). Indeed, the global trade in illegal wildlife products is rapidly increasing, and illicit sales of animal products (excluding fish and timber) totals between USD 7.8 and 10 billion each year (Haken 2011). The market has undergone significant changes in recent decades, for instance, illegal wildlife products are increasingly available on the Internet. The year 2011 saw more elephant poaching than any year on record (Hongfa and Thomas 2008). Both poaching in Africa and demand for wildlife products in Asia are increasing rapidly and they are believed to be linked. As this trade has become more lucrative, and as the demand for animal products as luxury items has grown, the traffickers involved are becoming increasingly sophisticated. They can be well-armed and prepared to pay significant bribes to facilitate their trade. In China, the illegal trade in tiger products fell in 2008, but also became more organized and covert, making it harder to detect and restrain (Hongfa and Thomas 2008). The governmental institutions that are weakened by such organized crime are usually responsible for small-scale hunting as well.

3.2 Poverty, conflicts and displacement

Poor communities in the developing world rely on bushmeat as a source of food and supplementary income. Their dependence on bushmeat, such as

elephants (Wittemyer 2011) and broader groups of forest species (Sayer et al. 2012) increases under economic hardships. Even if the Millennium Development Goal of halving the percentage of chronically hungry people is reached by 2015 (Estes et al. 2011), it is unlikely that the demand for bushmeat and the rate of harvest will decrease. In a context of political, economic and climatic instability, these pressures are unlikely to ease, especially as globalization increases connectivity in international markets.

Wars, uprisings, and other emergencies that create refugee populations, have significant effects on bushmeat harvest. Urban sales of protected species from Garamba National Park in the DRC increased dramatically when war increased the number of high-powered rifles in the area (de Merode and Cowlishaw 2006). The overall effect of war in the DRC was to increase the reliance on wood for fuel and bushmeat for protein (Draulans and Krunkelsven 2002). The Rwandan civil war depressed the prices of bushmeat but led to an increase in poaching of ungulates and accidental capture of gorillas (Plumptre et al. 1997).

People who are displaced by conflicts or other emergencies tend to rely on bushmeat, often because of dire nutritional needs and a lack of any other options. Resettled communities in Zimbabwe prevented anti-poaching scouts from accessing occupied land, enabling illegal hunters to operate freely (Lindsey et al. 2011). In northwestern Tanzania, bushmeat is sometimes the only available source of protein for refugees; it also offers a much-needed source of income, leading to intense hunting near the encampments (Jambiya et al. 2007).

3.3 Lack of alternatives to wild protein

A 68 kg adult male requires about 50 g of protein per day (FAO 2012). Overall, developing countries have malnutrition rates of about 15%. Centers of malnutrition have been shifting since 1990; at present there are more undernourished people living in Southern and Western Asia, sub-Saharan Africa, and Northern Africa than there are in Southeastern Asia, Eastern Asia and Latin America (Estes et al. 2011). Cost, taste and preference have less of an influence on which species are targeted when bushmeat is the primary means of fulfilling protein requirements. This is especially true where livestock husbandry is not feasible, e.g. in some remote forest areas of Central Africa and the Amazon Basin (Rushton et al. 2005). Using 30 years of data from Ghana, Brashares et al. (2004) found that those who depend on wild protein will substitute fish and bushmeat for one another, according to price and availability. The importance of bushmeat to the very poor is not limited to rural areas; in larger cities, bushmeat can be the cheapest source of protein and the protein staple for the poorest urban households (Nasi et al. 2011). Although wildlife farming has been proposed as a viable alternative, it is not economically viable compared to hunting or farming of domestic species, and is unlikely to reduce hunting, due to the high costs and cultural constraints (Mockrin et al. 2005). On the other hand, there may be options for hunting introduced or relatively robust species, which can absorb a higher intensity of hunting pressure. In the Brazilian Pantanal, introduced feral pigs are the primary target of hunters, and have reduced hunting of native game (Desbiez et al. 2011). In Africa, some species, such as the helmeted guinea fowl and the blue duiker or cane rat, breed quickly and can sustain a relatively high hunting pressure (Bennett et al. 2007).

3.4 Hunting regulations

Hunting regulations, in countries with large bushmeat markets, are often poorly enforced, but their usefulness suffers from perceptions that they infringe on local or traditional rights. Whether laws regulating the harvesting, marketing and consumption of bushmeat are working is often contested in many developing countries. Similarly, the value of community-based institutions that govern hunting practices is debated by experts and policy makers. In such contexts, bushmeat becomes a subject of conflict between conventional conservationists and local people.

The laws that govern bushmeat exploitation are usually aimed at a protected species or at an area where hunting is restricted or prohibited. There are often significant obstacles to enforcing the existing laws (Rowcliffe et al. 2004). The designation of protected areas and the establishment of hunting

regulations depend on good governance, but few successful models of wildlife management exist (Brown 2003). Enforcement often entails intervening in the markets in which animal products are traded, but such regulation may affect the hunters only indirectly. In China, the illegal hunting of wild cats is usually controlled through education and the confiscation of products. However, because hunters are difficult to identify, criminal charges are rarely filed against them. In general, the incentives to hunt may, for the hunter, outweigh the threat or actual enforcement of penalties. Organized criminals, in particular, may avoid penalties by withdrawing or resurfacing in relation to the weight of law enforcement during a given period of time (Hongfa and Thomas 2008).

The issues are further complicated by claims of traditional ownership, which, where accepted as valid in legal codes, are difficult to determine and enforce. In West Central Africa, there is little sensible distinction to be made between traditional and other uses of wildlife. But even where there is a relatively obvious difference between traditional versus immigrant hunters, improving weapons and access to regional markets are blurring the difference between subsistence and commercial hunting. Hunting interventions can come at various points along the supply chain, which can allay some fears about the negative impact on those who hunt for their own consumption (Crookes and Milner-Gulland 2006). Brown (2003) states that "presumed illegality at all levels is neither conducive to the development of participatory management models or to broader governance reform," and argues that in light of the livelihood dependence on bushmeat, legal channels for bushmeat trade must be created and monitored.

4 Management and intervention efforts: An overview

A truly sustainable use of bushmeat will require management changes at all scales, from local to international. Management practices will undoubtedly vary according to local conditions, but several consistencies have appeared in the efforts undertaken so far. This section examines some of the management practices that have been tested or proposed. Overall, the evaluation metrics are inadequate to draw conclusions; an improved system for tracking the results of reforms and projects would improve management.

Empty forests have concerned biologists and conservationists for decades. More recently, they have also become an imperative for development professionals, because as target animal populations decline, the income and nutrition they provide also decline (Brown 2003). The conservation and development communities have attempted a number of interventions in the bushmeat trade, with varying degrees of success, although there are only a few cases with published evaluations of the outcomes. The scale of investment is huge. For example, the World Bank and partners spent over USD 888 million on biodiversity projects in East Asia and the Pacific between 1999 and 2004 (World Bank Group 2004). The outcomes of such efforts are reported sporadically and often in descriptive rather than quantitative terms. It is particularly difficult to measure what effect, if any, projects have after the life cycle of the project. Many efforts have relied on temporary funding sources, yet a constant input of time and resources seems to be a key component of all interventions that have been dubbed successful. Some of the primary strategies include: enforcement and patrols; hunter education; community-based management; alternative income generation; and subsidies to encourage domestic meat production.

The strict control of licenses for arms and restricted sales of ammunition have limited hunting to subsistence extraction in Sarawak, Malaysia (Bennett and Robinson 2000). In extractive industries, such as logging, that bring hunters to new areas, strong leadership by the employer can reduce hunting pressure, but this requires a constant input of time and resources (Bennett and Robinson 2000). Elsewhere, confiscation of poached animal products has reduced the open trade (Hongfa and Thomas 2008). After poaching or hunting is controlled, some species can recover quickly, but others remain disrupted because they are k-selected or because they are specifically hunted for trophies (Steinmetz et al. 2010).

Hunter education programs have been attempted in Brazil (Constantino et al. 2008) and have sometimes seemed to reduce hunting pressure in focal areas (Miranda and Alancar 2007). It is usually impossible to distinguish hunter education from other interventions, since it is almost always included in projects, but the effectiveness is rarely measured.

Community-based management of hunted stocks has been successful for many species in northeastern Peru, though over-hunting of the most desirable and vulnerable species, such as tapir, persists (Bodmer and Puertas 2000). Such management efforts rely on the continual input of time and resources from NGOs. In some places such as the Udzungwa Mountains of Tanzania, wildlife stocks are too depleted to support community-based resource management at any level, and encouraging a transition to domestic meat is the only viable option (Nielsen 2006). There is likely a selection bias against good reporting of failed co-management efforts, but there is documentation of cases (e.g. in northern Cameroon) in which community-based management schemes have struggled with

inadequate legislation, poor planning and insufficient policy formulation (Mayaka 2002). The economic resources that forests provide are difficult to quantify, and the methodologies for doing so have been inconsistent and difficult to compare (Vedeld et al. 2004). Trying to understand trade-offs in income only complicates the picture. Nevertheless, there is a pervasive assumption in the literature that alternative income generation will reduce the exploitation of forest resources (e.g. Stoner et al. 2007b). This is problematic because there is little guarantee that small increases in income will dissuade bushmeat hunters from taking advantage of bushmeat. Once people can afford modern arms, the use of bushmeat may well decline with increasing income, as in Latin America (Wilkie and Godoy 2001) and Equatorial Guinea (Albrechtsen et al. 2006). However, where bushmeat conveys status or is preferred for taste or other cultural reasons, its consumption will rise steadily with income, as in Gabon (Wilkie et al. 2005) and even elsewhere in Equatorial Guinea (Fa et al. 2009). In the largest regional study in Africa, bushmeat consumption increases with wealth in urban areas and declines with wealth in rural areas (Brashares et al. 2011). Even where they are well-suited to the local economy, alternative income projects are also commonly subject to relatively short project cycles and may not have lasting results.

The idea of substituting alternative sources of protein is similarly problematic. In Gabon, household consumption of bushmeat is not related to the price of chicken and fish as potential substitutes (Foerster et al. 2011), although this trend varies by region, cultural practice and the segment of society. On a larger scale, the availability of fish does affect the use of bushmeat (Brashares et al. 2004), so the strategy may work well in certain situations. The farming of wild animals has also been considered as a viable option, but generally the economics of raising domesticated animals far outstrip those of raising wild animals (Mockrin et al. 2005). In particular cases, the commercial farming of wild species, such as porcupines in Vietnam, can function well if the stock populations are not obtained from the wild (Brooks et al. 2010).

Other variables, which have not been systematically addressed to evaluate their effects on poaching, are also likely to have impacts. For instance, clarifying and improving land tenure documents is a strategy in many conservation and development projects, and probably has an effect on local practices and tolerance of squatters and poachers, but this has not been evaluated to date.

5 Bushmeat harvest research: Current knowledge gaps and research priorities

This section focuses on the specific objective of improving resource management and the sustainability of bushmeat harvest. The emphasis is on research that advances our understanding of the dynamic connections and dependencies among hunters, prey and forests. Of particular interest are the potential responses of bushmeat markets and resources to predicted climate change, urban expansion and other socio-environmental shifts.

Appendix 1 presents the most pressing research gaps in our existing knowledge. Attention to these issues will substantively advance the aim of sustainably harvesting bushmeat. Asia, the Neotropics and Africa are treated separately because their research needs differ. Overall, Asia lags far behind the other two regions in all aspects of research. In broad terms, the effect of bushmeat on livelihoods is better understood in Africa than in the Neotropics, and the ecological effects of hunting and defaunation are better understood in the Neotropics. The research topics listed for each region reflect these generalizations, and the specific recommendations for research sometimes reflect the quality of the basic information. For example, more sophisticated analyses of livelihoods are possible in Africa because better information exists. The list is organized to echo the themes stated in Section 1 of this paper, namely: the effects on livelihoods, in terms of nutrition and income; the effect on animal populations in terms of extraction rates and sustainability; and the impact of bushmeat harvest on ecosystem function.

5.1 Five critical knowledge gaps and research opportunities

Asian tropics. Overall, there is much less information available on bushmeat harvest in the Asian tropics, especially outside of Borneo, and in parts of China. There is a critical need for more research efforts focused on other forested regions of the Asian tropics, such as the Mekong River Basin (Burma, Cambodia, Laos and Vietnam).

Fallows. There is a need for a better understanding of the capacity of secondary forests, fallows and other non-primary forest habitats in order to sustain game populations. Much of the existing research has focused on species that tend to be found in primary forest, which has resulted in a neglect of the surrounding matrix as a source of bushmeat, and of the potential to sustainably manage these areas.

Evaluation of projects. The literature is very sparse in terms of evaluating projects, and there is a critical need for more research on the effectiveness of management and intervention efforts.

Ecosystem function. The long-term effects of defaunation on ecosystem function are poorly understood and additional research is needed, especially for the Afro- and Asian tropics.

Expanding the spatio-temporal scale, and improving the analytic sophistication of studies. Several studies are limited to individual seasons and focus on very specific areas, including those used in meta-analyses. An increased collaboration between field researchers and modelers is crucial to improving the accuracy of long-term forecasts and predictive models. Improved access to data to produce syntheses, is also necessary.

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Appendix 1
Wild meat harvest research: Knowledge gaps and research opportunities

	Livelihoods	Game populations	Ecosystem function
ASIA	• Create commodity chains for the largest wildlife markets and most-hunted species • Distinguish between wildlife harvest for luxury and subsistence markets	• Collect baseline data on wild game populations and offtake rates • Synthesize available information for the region and provide wide-ranging estimates of offtake	• Evaluate ecosystem function and diversity in defaunated sites throughout Asia, establish a network of sites along a gradient of ecological situation and anthropogenic effects
NEOTROPICS	• Expand the temporal scope of studies, and target missing socioeconomic and economic settings to generate more case studies for meta-analysis • Improve profiling of hunter populations, especially to compare local and immigrant hunters	• Develop management recommendations and quantify sustainable offtake for secondary forests, fallows and other matrix habitat • Broaden the scope of wildlife population modeling efforts to include multiple species and human dynamics • Compare population resilience and likely demand for various species • Explicitly consider spatial scale in offtake statistics, e.g. regional source–sink dynamics • Improve the Redford index of sustainable yield by incorporating multiple species and hunting dynamics • Evaluate hunting restrictions and reintroductions specifically aimed at frugivores	• Examine long-term effects of defaunation on nutrient cycling • Determine the effect of the reduced recruitment of zoochorous fruit trees on the future capacity to support human uses • Evaluate the diversity of plant species in defaunated areas. • Explore the potential for Payments for Ecosystem Services • Examine the role of game species in structuring vertebrate communities • Evaluate the effects of hunting on non- target species

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Appendix 1. Continued

	Livelihoods	Game populations	Ecosystem function
AFRICA	• Expand the temporal scope of studies, and target missing socioeconomic and economic settings to generate more case studies for meta-analysis • Improve data on economic (rather than nutritional) reliance on bushmeat harvest • Improve our understanding of consumer preferences for domestic and wild meat • Identify the interaction between hunting for bushmeat and other uses (e.g. medicinal and ornamental) • Incorporate local heterogeneity and social differentiation into forest income assessments • Model the future demand for bushmeat based on projections of urban growth • Model the tradeoffs of wild and domestic meat under future market scenarios • Establish a quantitative relationship between hunting effort and alternative sources of income • Compile best practices from realized projects in sustainable harvest • Contextualize all policies within the bushmeat commodity chain, i.e. specifically • identify how stakeholders along the chain are affected • Develop incentives for managers of logging concessions to manage bushmeat harvest on their land • Explore strict bans on threatened game paired with a legal avenue for the sale of common and more robust species	• Develop management recommendations and quantify sustainable offtake for secondary forests, fallows and other matrix habitat • Improve basic biology for hunted and unhunted African forest mammals, such as reproductive seasonality, maturation, fecundity and feeding ecology • Report on basic ecology and population status of the most hunted species, e.g. blue duiker, which are understudied compared to threatened game • Conduct long-term demographic studies for more species and locations in hunted and unhunted sites • Additional large-scale studies with comparable methodologies are needed in different habitats along the defaunation gradient • Compare population resilience and likely demand for various species • Examine compensatory behavior within mammalian communities • Broaden the scope of wildlife population modeling efforts to include multiple species and human dynamics • Explicitly consider spatial scale in offtake statistics, e.g. regional source-sink dynamics and their underlying biological mechanisms • Examine the relative proportions of ungulates and rodents in offtake as an indicator of site overexploitation.	• Examine long-term effects of defaunation on nutrient cycling • Determine the effect of the reduced recruitment of zoochorous fruit trees on the future capacity to support human uses • Evaluate the diversity of plant species in defaunated areas. • Explore the potential for Payments for Ecosystem Services • Examine the role of game species in structuring vertebrate communities • Evaluate the effects of hunting on non- target species

CIFOR Occasional Papers contain research results that are significant to tropical forest issues. This content has been peer reviewed internally and externally.

Food security is increasingly becoming a priority for tropical countries. This has led to reconsideration of the need to find systems and practices of sustainable harvest, consumption and trade of bushmeat and other wildlife products. This paper provides a synthesis of information found in the expanding global literature on the many dimensions and functions of game species, bushmeat and other game resources. Much research effort has focused on documenting and measuring the impact of bushmeat harvesting on populations of targeted game species. This has resulted in an emphasis of conservation effort on the protection of game species and the criminalization of hunting, bushmeat trade and consumption. Despite decades of official bans on bushmeat trade and consumption, some socioeconomic studies have shown that bushmeat is often the main source of protein and income for low-income urban and rural families in some tropical countries. Similarly, the role of large and small-bodied game species in the sustainable provision of seed dispersion and other ecosystem services are underlined by some ecological and conservation biology studies. A great diversity of complex management systems of game species in forests and on agriculture land are reported by some ethnographic studies. The encouraging results from some bushmeat studies are an incentives to conduct evidence-based studies that can generate knowledge and information that can help policy-makers to make informed decisions.

In the majority of tropical countries, relatively little research has been undertaken based on the premise that bushmeat is an important resource provided by forest ecosystems, and aimed at devising strategies for the management and sustainable use of bushmeat. Research on bushmeat harvest is unevenly distributed, thematically and institutionally, across the three main regions of tropical forest — the Neotropics, Afrotropics and Asian tropics. Given the current fragmented understanding of the ecological, socioeconomic and cultural dimensions of bushmeat harvest, there is limited technical-scientific information on the relationship between game species and the provisioning of ecosystem services, as well as the capacity for bushmeat to enhance or constrain adaptive responses to ongoing socio-environmental change (e.g. climate change, urbanization, land-use change, etc.). These issues are crucial for any effort to ensure human well-being and environmental conservation in tropical forests.

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