

Chapter 24

Bushmeat and Emerging Infectious Diseases: Lessons from Africa

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Introduction

Emerging infectious diseases (EIDs) are human diseases that are either newly discovered or are increasing in incidence or geographical range. Some diseases, such as measles, sleeping sickness, and bubonic plague, emerged in prehistoric or ancient times (Babbott and Gordon 1954; Hays 2005; Steverding 2008), whereas others, such as Ebola virus, Nipah virus, and SARS, emerged more recently (World Health Organization 1978; Chua et al. 2000; Guan et al. 2003). The trend of EID emergence is accelerating: over 300 distinct emerging disease events have been recorded in the last six decades and more than 35 new infectious diseases have emerged in humans since 1980 (Lederberg et al. 2003; Jones et al. 2008).

Upwards of 75 % of EIDs in humans are of zoonotic origin, which means the pathogen originates in animals and is transmitted to humans (Taylor et al. 2001; Jones et al. 2008; Karesh and Noble 2009). Although many zoonotic pathogen spill-overs arise in domestic animals, including livestock, the majority (71.8 %) of zoonotic EIDs arise from wildlife species (Jones et al. 2008). In many developing countries, domesticated animals live in close proximity to wildlife. This facilitates the movement of pathogens between them and to humans through interactions with sylvatic disease cycles or through two-step wildlife-to-domestic animal-to-human emergences. Examples include rabies infections, which move between wildlife and domestic dogs, with recurring spillovers to humans; and the Henipah viruses, in which *Pteropus* flying foxes are the reservoir host and domestic pigs or horses are

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amplifier hosts from which spillovers to humans have been documented (Childs et al. 2007; Daszak et al. 2007). Not surprisingly, the most devastating pandemics in human history, the Black Death, Spanish influenza, and HIV/AIDS, were all caused by zoonoses from wildlife (Morens et al. 2008).

Zoonotic diseases can spill between animal hosts and humans in a variety of ways, including through (a) shared vectors, such as mosquitoes for malaria, (b) indirect contact, such as exposure to rodent feces in a peridomestic setting, or (c) direct contact with an animal through consumption, animal bites, scratches, body fluids, tissues, and excrement (Wolfe et al. 2005a). Most pathogens infecting animals fail to make the jump into humans, but 33 % of zoonotic pathogens (~286 out of 868 zoonotic pathogen species studied) that have spilled over are known to be transmissible between humans (Taylor et al. 2001). Of all EIDs, zoonotic spillovers from wildlife have been identified as the most significant, growing threat to global health (Cleaveland et al. 2007; Jones et al. 2008).

Recent evidence highlights the link between infectious diseases and biodiversity loss, land use changes, and habitat fragmentation (Cleaveland et al. 2007; Maganga et al. 2014; Gottdenker et al. 2014). Although additional research on the relationship between habitat degradation and EIDs is needed, Gottdenker et al. (2014) reviewed 305 studies incorporating a broad variety of diseases and found that the most common land use change types related to zoonotic disease transmission were deforestation, habitat fragmentation, agricultural development, irrigation, and urbanization. Functionally, the mechanisms influencing disease spillover include disruption of food web structures, changes in host–pathogen interactions, and mixing of pathogen gene pools resulting in increased pathogen genetic diversity (Jones et al. 2013). Many studies have shown that habitat fragmentation and biodiversity loss correspond to an increase in disease and pathogen abundance and diversity within a host species (Allan et al. 2003; Gillespie et al. 2005; Keesing et al. 2006; Salzer et al. 2007; Cottontail et al. 2009; Young et al. 2014). Specifically, the emergence or re-emergence of many zoonotic diseases including yellow fever, Lyme disease, hantavirus pulmonary syndrome, Nipah virus encephalitis, influenza, rabies, malaria, and human African trypanosomiasis have been linked to anthropogenic habitat changes (Jones et al. 2013).

Many of these human environmental changes are occurring in sub-Saharan Africa where human bushmeat activities have been linked to numerous virulent disease outbreaks, including Ebola (Leroy et al. 2004a), HIV (Van Heuverswyn and Peeters 2007), and monkeypox (Rimoin et al. 2010). Pathogen spillover from bushmeat can occur through consumption; however, the main risks are associated with exposure to body fluids and feces during handling and butchering (Kilonzo et al. 2014; Paige et al. 2014). Historically, when a spillover occurred, the likelihood of an epidemic was limited because hunter-gatherer tribes were generally small and widely dispersed, hampering disease transmission between groups of people. Once agricultural expansion occurred, human population densities increased, and people became better connected, diseases could spread more easily. As a result, transmissions of infectious diseases from animals to humans have led to devastating outcomes

across the globe (LeBreton et al. 2006). EIDs cause hundreds of thousands of deaths annually (Bogich et al. 2012). Some outbreaks have spread across large regions and became pandemics, costing the global economy tens of billions of dollars (e.g., SARS, H5N1, the 2014–2015 West African Ebola outbreak) and bringing entire nations to the brink of economic collapse.

In this review, we explore the links between bushmeat-related activities and EIDs in sub-Saharan Africa, where the vast majority of African emerging infectious zoonotic diseases occur (Jones et al. 2008). The recent Ebola outbreaks have highlighted the potential role of bushmeat as a source of pathogens, but a comprehensive review of the different pathogens that may emerge from wildlife through bushmeat-related activities is lacking. Although we are in no way suggesting that this issue is more important than other pressing health crises in sub-Saharan Africa (such as malaria prevention/treatment and improving healthcare infrastructure), we argue that a better assessment of the public health threats associated with this human-wildlife interaction is warranted and necessary to improve management of future disease outbreaks.

Bushmeat

The term “bushmeat” refers to the meat derived from wild animals for human consumption (Milner-Gulland and Bennett 2003) (Fig. 24.1). It includes a wide range of animals, such as invertebrates, amphibians, insects, fish, reptiles, birds, and mammals, including as many as 500 species in sub-Saharan Africa (Ape Alliance 2006). Although research has focused largely on mammals and, to a lesser extent, birds, theoretically any wildlife species harvested for bushmeat could be a potential source of zoonotic disease that can spillover during the hunting, butchering, and preparation process (Wolfe et al. 2000; Karesh and Noble 2009). Hunters face risk of injury from live animals, which might allow animal blood to enter the hunter’s bloodstream through open wounds. While small animals can be carried in bags, large animals are commonly carried on the shoulder or back, bringing the hunter in close contact with the animal and facilitating transfer of body fluids (LeBreton et al. 2006). The highest risk of disease transmission occurs during the butchering of animals, e.g. skinning, opening of the body cavity, removal of organs, and cutting of meat. More people butcher than hunt animals (83 % and 42 %, respectively, LeBreton et al. 2006) and butchering involves the use of sharp tools, which may lead to cuts during the process. Subramanian (2012) found that 38 % of respondents cut themselves on a regular basis during butchering. Women are especially at risk of disease transmission as they engage more often in butchering and in food preparation than men. In discussing the links between bushmeat and disease, we refer to this all-encompassing suite of risky behaviors as “bushmeat-related activities.”

Nonhuman primates, rodents, and bats have all been linked to the spillover of zoonotic diseases into humans (Cleaveland et al. 2007; Jones et al. 2008; Kilonzo

Fig. 24.1 Bushmeat being smoked in rural South Sudan; photo credit Adrian Garside



et al. 2014). A review of the West and Central African bushmeat literature including market, offtake, and consumption surveys documented a total of 177 species from 25 orders that were harvested for bushmeat, including 134 (76 %) mammal species, 24 (14 %) bird species, 18 (10 %) reptile species, and 1 (<1 %) amphibian species (Taylor et al. 2015). Among mammals, the largest group was primates (48 species) including western gorillas (*Gorilla gorilla*), bonobos (*Pan paniscus*), and common chimpanzees (*Pan troglodytes*), followed by ungulates (34 species), carnivores (22 species), and rodents (16 species). In terms of biomass offtake, however, ungulates are generally the most prominent group. Although the Taylor et al. (2015) study is very comprehensive, it only included studies that: (1) provided a quantitative measure of bushmeat offtake, consumption, and/or market availability/sales; (2) used non-biased data collection methods and systematically sampled settlements/hunters to prevent selection bias; (3) identified carcasses to the species level; and (4) recorded either the number of carcasses or the total biomass (kg). For a more inclusive and general review of existing Central African bushmeat studies, see Wilkie and Carpenter (1999), and for West African studies, see Schulte-Herbrüggen (2011). Fa et al. (2006) found that of the approximately one million carcasses traded in the Cross-Sanaga region of Nigeria and Cameroon, 99 % were mammals; of which around 40 % were ungulates, 30 % rodents, and nearly 15 % primates. However, as wildlife populations become depleted, such as near urban areas and intensively used agricultural landscapes, smaller bodied mammals comprise a larger share of hunters' offtake (Bowen-Jones et al. 2003; Schulte-Herbrüggen et al. 2013a).

Livelihood Importance

Humans have hunted wild animals for consumption and to protect their crops for millennia (Shipman et al. 1981; Grubb et al. 1998; Davies et al. 2007), and it remains an important source of food and income security among rural communities today (de Merode et al. 2004; Brashares et al. 2011). Bushmeat is an important source of animal protein in many West and Central African countries, with up to 90 % of total animal protein consumption coming from wild animals (Fa et al. 2003). Overall, the contribution of bushmeat to protein and food security is generally lower in urban than rural areas and is highest among remote rural communities (Brashares et al. 2011). For example, the relative importance of bushmeat in the diet of rural Gabonese households ranged from 13 % of total household consumption value in a village near a town to 25 % in a remote community (Starkey 2004). Similarly, for rural Equatorial Guinea, Allebone-Webb (2008) showed that bushmeat consumption contributed 43 % to total protein consumption in a village with poor transport links, but only 18 % in a village with good connections. In remote Cameroonian communities with very few opportunities for purchasing alternative protein sources, bushmeat comprised 80–98 % of animal protein consumption (Muchaal and Ngandjui 1999). In rural communities with relatively good market access and low levels of bushmeat consumption, the importance of bushmeat for food has been shown to increase seasonally during the agricultural lean season (e.g. the planting season between harvests) when farming households receive little income (Dei 1989, de Merode et al. 2004, Schulte-Herbrüggen et al. 2013b) and during the dry season when fish is not available (Poulsen et al. 2009). Bushmeat is also an important source of nutrients, especially among children. Evidence from rural Madagascar shows that removing bushmeat consumption would result in a 29 % increase in the number of children suffering from anemia and triple the cases of anemia among children in the poorest households (Golden et al. 2011).

Most hunters sell at least part of their harvest making it an important source of income, especially where alternative income-generating activities are lacking. The importance of bushmeat in household economies varies across sites and individual hunting households, ranging from 38 % to more than 90 % of the total cash income earned (reviewed in Schulte-Herbrüggen 2011). In rural Gabon, hunting accounts for up to 72 % of household incomes, with the proportion rising in poorer, more remote communities (Starkey 2004). Hunters are also more likely to sell large animals and keep small animals for their own consumption, because the latter fetch a lower price per animal and may be less marketable (van Vliet and Nasi 2008). Finally, households facing income shortages during the agricultural lean season and requiring cash income to pay for urgent expenditures, such as hospital bills, are more likely to sell bushmeat than keep it for own consumption (de Merode et al. 2004).

Overall, income from bushmeat sales can be lucrative and compare favorably with alternative work in many rural places. Vega et al. (2013) found that commercial hunters in Equatorial Guinea generated a mean of US\$2000 per year from bushmeat sales.

Hunters supplying markets in Central African logging concessions earned twice the income of junior technicians working at a logging company (Tieguhong and Zwolinski 2009). Rural Kenya hunters can earn 2.5 times the average salary in the area (Fitzgibbon et al. 1995), and Ghanaian hunters can earn income similar to that of a graduate entering Wildlife Service, and up to 3.5 times the government minimum wage (Ntiamo-Baidu 1998). Very successful Zambian hunters have been reported earning just below the mean annual income in a single hunting trip (Brown 2007).

The sale of bushmeat historically occurred at a local level, but with increased transportation routes and globalization, the bushmeat trade is expanding to supply urban and international demand. In the past, novel pathogens entering the rural communities may not have spread beyond the community, but this is no longer the case as remote rural areas are connected to urban areas, and increased global trade networks and air travel increases the risk of disease transmission worldwide (Brashares et al. 2011). This expanding trade network links hunters to consumers, and with many people along this commodity chain coming into contact with bushmeat, the opportunity for disease spillover can occur at many points. For example, the commodity chain supplying bushmeat to an urban market in Ghana includes hunters, wholesalers, market traders, restaurant owners, and consumers (Mendelson et al. 2003). The bushmeat commodity chain supplying an urban market in Democratic Republic of the Congo is comprised of hunters, porters who carry the meat to the road, the bicycle traders who transport the meat into town, and the market-stall owners who sell the bushmeat to consumers (de Merode and Cowlshaw 2006). A recent study from Ghana estimates that a minimum of 128,000 bats are sold each year through a commodity chain that stretches up to 400 km and involves multiple vendors (Kamins et al. 2011a). In Zambia, Mozambique, and Malawi, well-developed and complex rural-urban trade supply networks link rural hunters to urban consumers who are willing to pay high prices for bushmeat (Barnett 1997). Understanding commodity chains is important, as pathogens likely remain viable for some period after an animal is killed. For example, Prescott et al. (2015) demonstrated that Ebola virus remains viable on monkey carcasses for at least seven days, with viral RNA detectable for 10 weeks.

Scale of Bushmeat Harvest in Sub-Saharan Africa

Bushmeat has become a multi-million dollar business due to a growing human population and is now serving both subsistence and trade objectives. Harvest volumes have been estimated at 12,000 tones per year in the Cross-Sanaga rivers region of Nigeria and Cameroon (Fa et al. 2006), 120,000 tones per year in Côte d'Ivoire (Caspary 1999), 385,000 tons per year in Ghana (Ntiamo-Baidu 1998), and at total of 1–4.9 million tons per year in Central African forests (Wilkie and Carpenter 1999; Fa et al. 2002).

However, it is important to recognize that our understanding of the scale of bushmeat harvest is limited by the availability of information and hence current regional

harvest estimates might underestimate actual harvest volumes. Despite substantial effort in recent years, our knowledge is still site-specific and data are lacking from many regions. Most surveys have been restricted to relatively small areas or market catchments from which national estimates were extrapolated. Research efforts have focused on Central Africa with some data available for 60 % of countries compared to 30 % of West African countries (Taylor et al. 2015). A large number of sites with detailed bushmeat data are concentrated in the Cross-Sanaga region of Nigeria and Cameroon, where Fa et al. (2006) collected market data at 86 sites, hence presenting a geographical bias in our understanding of bushmeat harvest. Furthermore, the majority of available data samples (79.3 % and 53.6 %, in West and Central Africa, respectively) identified by Taylor et al. (2015) come from market surveys with poorly defined catchment areas, compared to offtake and consumption surveys. Strong variation between individual estimates highlights the problems with extrapolation of survey data to national or regional levels and the effects of sampling strategies (hunter versus market surveys), timing of survey (open season versus lean season), survey location, and extrapolation methods. Individual figures should therefore be treated with caution, but the overall message remains: bushmeat is harvested at an enormous scale exposing those involved in the bushmeat commodity chain to zoonotic diseases.

Drivers of Increased Bushmeat Hunting and Disease Risks

The current scale of bushmeat hunting is primarily the result of socio-demographic changes (Wilkie and Carpenter 1999). Africa's human population has risen from 0.2 billion in 1950 to 0.9 billion in 2013 and is expected to rise to 2.2 billion by 2050 (United Nations 2013). Where alternative sources of animal protein and income are scarce, human population growth has been linked to increasing hunting intensity (Brashares et al. 2001).

Bushmeat has been and remains a staple source of animal protein among the rural poor, yet recent attention has focused on urban consumers of bushmeat as a driver of increased hunting. Urban consumers generally have a range of meat sources from which to choose, but value bushmeat for its taste, cultural connotations, and as a luxury food item (Fa et al. 2009). While urban consumers generally consume less bushmeat than rural consumers (Brashares et al. 2011), urban populations in Africa have increased dramatically from about 15 % of the total population in 1950 to 40 % in 2014 (United Nations 2014) and have created a strong demand for bushmeat and hence market for rural hunters.

The increasing demand for bushmeat has been accompanied by changes in hunting technology and improvements in hunting efficiency. Traditional hunting tools, such as nets and bow and arrow, have been replaced with more modern tools of guns and snares. Modern guns have an up to 25-times higher rate of return compared to traditional weapons (Wilkie and Curran 1991), substantially increasing the ease and cost-effectiveness of hunting (Alvard 1995). This enables hunters to catch more

animals and sell a larger part of their catch (Bowen-Jones and Pendry 1999; Bowen-Jones et al. 2003; Nasi et al. 2008).

Hunting efficiency has also improved as remote forests have become more accessible through the construction of logging roads and improved transportation (Wilkie et al. 1992; Auzel and Wilkie 2000). For example, after the construction of 140 km of logging roads in northern Congo, the average time for a hunting trip was reduced from 12 to 2 hours (Wilkie et al. 2001). Development of rural businesses, such as timber companies, attracts workers and their families to remote locations, increasing bushmeat demand, especially when no hunting regulations are in place and alternative protein sources are not provided (Auzel and Wilkie 2000; Bennett and Gumal 2001; Poulsen et al. 2009). The effect of logging company presence on hunting pressure was documented in Gabon where ape populations decreased 50 % between 1983 and 2000 as a result of hunting (Walsh et al. 2003). In addition, agricultural expansion and mining have exerted a strong force in changing the African landscape and influencing human migration patterns (Norris et al. 2010). Due to increased access, people are brought into closer contact with wildlife, which facilitates accessibility to bushmeat hunting and makes transportation of bushmeat from rural to urban areas easier and more cost-effective (Wolfe et al. 2005a).

Along with increased ease of transportation comes the opportunity for bushmeat to be traded on the international market. The international trade in bushmeat has recently gained attention as both a driver of bushmeat hunting and the cross-border spread of zoonotic diseases. Illegal wildlife trade is the second-largest black market worldwide, involving millions of animals and estimated to be worth US\$50–150 billion per year (United Nations Environment Programme 2014). Case studies at airports screening passenger luggage for bushmeat estimated that approximately 5 tons of bushmeat per week arrive at Paris Roissy-Charles de Gaulle airport (Chaber et al. 2010) and 8.6 tons per year at Zurich and Geneva airports (Falk et al. 2013). As bushmeat hunting, globalization, and human interconnectedness increase, the potential for zoonoses leading to EIDs also increases. This risk was highlighted when retroviruses (e.g., simian foamy virus) and herpesviruses (cytomegalovirus and lymphocryptovirus) were found in confiscated primates at US airports (Smith et al. 2012).

Bushmeat as a Source of Zoonotic Diseases in Sub-Saharan Africa

Indisputable evidence of the transmission of pathogens from wildlife to humans exists only for relatively few cases because the standard of proof is very high. Nevertheless, the evidence for spillovers is very strong and many pathogens can be classified as very likely to spillover (Jones et al. 2008; Kilonzo et al. 2014). Furthermore, countless pathogen species of zoonotic potential will likely be discovered as surveillance increases (Taylor et al. 2001; Jones et al. 2008). Our close phylogenetic relationship with nonhuman primates increases the likelihood that pathogen spillover from these animals to humans will cause infection (Childs et al. 2007).

Moreover, it is not surprising that many studies have focused on spillover events from nonhuman primates to humans given the high prevalence of these largely diurnal mammals in the bushmeat trade (Taylor et al. 2015). For instance, nonhuman primates of the family Hominidae include the Gorillinae and Paninae, which show a genetic difference of only 2 % or less with humans (Gonzalez et al. 2013), and members of these subfamilies share many morphological, physiological, and ecological features that may have a direct role in the transmission of infectious diseases (Davies and Pedersen 2008). Cleaveland et al. (2007), in their assessment of the risk of disease emergence by taxa, found that the relative risk of disease emergence was highest for bats, followed closely by primates, then ungulates and rodents. There have been surprisingly few studies of the connection between hunting of birds or other vertebrates and EIDs, especially in Africa, but surveillance for zoonotic pathogens in African birds is strongly needed (e.g., for avian influenza tracking see Simulundu et al. 2011, 2014).

The characteristics of different species may render them more or less susceptible to hunting. Behavioral traits such as communal nesting, large-group living, loud acoustic performances, and a diurnal lifestyle—which are found in many primate species—may facilitate the detection and harvesting of several individuals at one time (Bodmer 1995). Taste preferences for certain species influence hunters' decisions as do attempts to maximize returns by preferring large-bodied animals that provide more food or fetch a higher price when sold than small-bodied species (Bodmer 1995). Bats, especially the larger fruit bats popular in the bushmeat trade, are susceptible to hunting because they are often found in large, sometimes vocal groups that are visible during the day or in high concentrations in caves (Mickleburgh et al. 2009). Increased human encroachment in recent decades (Kamins et al. 2011b) has driven some bat species to become peridomestic (O'Shea et al. 2011; Plowright et al. 2011), which renders them easy targets for hunting. Finally, sick animals may be less successful in evading hunters and hence more easily hunted, thereby increasing the risk of disease transmission to hunters.

In addition to the behavioral traits that may influence which species are hunted, physiological traits of these species may make them more likely to harbor and transmit diseases. For example, bats, which are present in the bushmeat trade and comprise the highest risk among all wildlife for harboring emerging diseases (Cleaveland et al. 2007), present unique traits that suit them to hosting pathogens. These traits include: (1) relatively long lifespans for their body size (Munshi-South and Wilkinson 2010), which may facilitate pathogen persistence for chronic infections; (2) flight, which allows movement and dispersal over long distances and which creates high body temperatures that may select for co-evolution with viruses that can live at febrile temperatures and are therefore highly virulent in humans (O'Shea et al. 2014); (3) physiological similarity across sympatric species that roost together in high densities enabling pathogens adapted to any of the sympatric species to spillover to others (Streicker et al. 2010); and (4) regulation of their immune systems in such a way as to make them more likely to host, but remain unaffected by viral pathogens, serving as the reservoir host for emerging and highly virulent viruses (Baker et al. 2013).

Despite the fact that pathogens are common and often occur in high numbers in basically all animals, only a relatively small proportion of these pathogens will spillover to humans (Cleaveland et al. 2007). That said, when spillover events do occur, they can be not only deadly but costly. For example, the United Nations Development Program (2015) has estimated that West Africa as a whole may lose US\$3.6 billion per year between 2014 and 2017 due to the 2014–2015 Ebola outbreak. This loss stems from the cumulative effects of closed borders, decreased trade, decreased foreign direct investment, and decreased tourism, resulting in increased poverty levels and food insecurity.

To understand the dynamics of spillover events and risks in relation to the pathogen, a number of factors must be considered, including: (1) the evolutionary history of the pathogen, (2) how the pathogen is maintained among its wildlife host(s), (3) how the pathogen is transmitted across a species barrier, (4) whether a productive infection is produced in the new host, (5) whether that infection produces significant disease in that host, and (6) whether morbidity and/or mortality levels in the secondary host are sufficient to be considered significant (Childs et al. 2007). From this, it follows that emerging pathogens are not an arbitrary selection of all pathogens. Becoming established in a human host typically requires adaptations, often for increased virulence, as has been documented in HIV (Wain et al. 2007; Etienne et al. 2013). Generalist pathogens have the ability to infect more than one host species and have higher relative emergence risk than pathogens that are very host-specific (Cleaveland et al. 2007); this is especially true for pathogens that can infect species in more than one taxonomic order. One example of this generalist “broad” host range is found in the newly described African henipavirus, which can enter and infect cells of nonhuman primates, bats, and humans (Lawrence et al. 2014).

Of particular importance for understanding bushmeat-related spillover events is whether a wildlife species is a natural or incidental pathogen host. Natural or reservoir hosts are a natural part of the pathogen life cycle and may maintain the infectious pathogen for prolonged periods of time, often without showing symptoms. In contrast, an incidental or dead-end host may be infected by the pathogen and may even transmit it, but it is not a part of the normal maintenance cycle of the pathogen and is more likely to be affected by it than natural hosts. For example, contact with sick common chimpanzees and western gorillas has been tightly linked to Ebola virus spillover in several outbreaks (Leroy et al. 2004b). Like their human cousins, these great apes are largely considered incidental or dead-end hosts for this virus and do not maintain it long-term in nature. In the case of this deadly filovirus, understanding what species are true reservoirs (likely fruit bats in the family Pteropodidae; Pourrut et al. 2007, 2009; Hayman et al. 2010, 2012) and the spillover events between these reservoirs and other mammals (including apes, carnivores, and ungulates; Leroy et al. 2004a) will prove critical to mitigating the components of disease transmission that are due to bushmeat-related activities. Unfortunately, it is often difficult to definitively determine the natural host(s) of a particular pathogen as it requires, in descending order of importance, isolation of the agent from individuals of the target species, detection of pathogen-specific nucleic acid sequences from

individuals, and serological evidence that an individual has been exposed previously. Indeed, the study of reservoir systems and how infectious agents move between and within them can be complex, requiring rigorous and sophisticated analyses of multiple interrelated variables (Gray and Salemi 2012; Viana et al. 2014).

Descriptions of the types of pathogens potentially encountered through bushmeat-related activities can be found below, with several important and well-studied examples described in more detail. In their review of global trends in EIDs, in which they separately listed each antimicrobial pathogen strain that has recently emerged, Jones et al. (2008) report that the vast majority of pathogens involved in EIDs are bacterial or rickettsial, followed by viral or prion, then protozoa, fungi, and helminths. Other studies have ranked viruses as more prevalent (Taylor et al. 2001; Woolhouse et al. 2005; Cleaveland et al. 2007). In Jones et al.'s (2008) analysis of 335 EID events between 1940 and 2004, only four EIDs list bushmeat as the driver; other significant drivers were socioeconomic factors such as human population density. These four bushmeat-related EID events were all significant events; all due to viruses (Ebola virus, human immunodeficiency virus-1, monkeypox virus, and SARS), suggesting that viruses are the most important pathogens in regard to spillover due to bushmeat-related activities (see also Kilonzo et al. 2014). We review the literature from sub-Saharan Africa in relation to bushmeat species by pathogen type (viruses, bacteria, helminths, protozoa, fungi, and prions), noting the significant potential for pathogens not yet associated with bushmeat-related activities to also be involved. Very few studies have considered all of the potential zoonotics in a region or in a taxonomic group. Magwedere et al.'s (2011) comprehensive study of zoonotics in Namibia is an exception.

Overview of Pathogens Related to Bushmeat Activities

Table 24.1 summarizes these pathogens by bushmeat host taxonomic group, conservatively listing only those species/pathogen combinations that have been tied strongly to spillovers from wildlife to humans via bushmeat-related activities and recognizing that this link is often putative and difficult to establish. Thus, Table 24.1 does not include some of the potential but not demonstrated spillover risks of poorly studied groups such as helminths and protozoans. Furthermore, due to their close genetic relationship with humans, common chimpanzees and western gorillas may share many pathogens of all varieties with humans, but the direction of spillover is not always clear (e.g. tourist interactions may spread disease from humans to apes) and much of these data are not discussed herein. Also not included in the table are studies where pathogens are not determined to species and, consequently, the bushmeat host–human link is unclear, or where exposure would be via an insect vector, which could be encountered when handling bushmeat. While we have attempted a very thorough treatment of pathogens that meet our criteria for inclusion in the table, it is possible that some relevant studies have been missed.

Table 24.1 Bushmeat species and zoonotic pathogens for which strong evidence for spillovers via bushmeat-related activities exists (see criteria for inclusion in text)

Bushmeat species	Pathogen	Location	References
Great Apes (Chimpanzee, Bonobo, Gorilla) ^a	Zaire Ebolavirus (V)	Cameroon, Gabon, Republic of Congo	Leroy et al. (2004a, b)
<i>Pan troglodytes</i> (Common chimpanzee)	Tai Forest Ebolavirus (V)	Côte d'Ivoire	Le Guenno et al. (1995), Wyers et al. (1999)
	HIV-1/SIVcpz (V)	Cameroon, Democratic Republic of the Congo, Tanzania	Santiago et al. (2002), Worobey et al. (2004), Van Heuverswyn et al. (2007)
	HLTV/SLTV-1 (V)	Central & Eastern Africa	Gao et al. (1999), reviewed in Sharp and Hahn (2010), Peeters et al. (2013)
	Simian Foamy Virus (V)	Cameroon, Côte d'Ivoire, Gabon, Republic of Congo, Tanzania	Calattini et al. (2006), Liu et al. (2008)
	<i>Strongyloides fulleborni</i> (H)	Gabon	Mouinga-Ondémé et al. (2012)
<i>Pan paniscus</i> (Bonobo)	<i>Entamoeba histolytica</i> (P)	Tanzania	Gillespie et al. (2010)
	<i>Balanitium coli</i> (P)	Central African Republic, Tanzania	Lilly et al. (2002), Gillespie et al. (2010)
	<i>Giardia intestinalis</i> (P)	Guinea Bissau	Sak et al. (2013)
	<i>Bacillus anthracis</i> (B)	Côte d'Ivoire	Leendertz et al. (2004)
	HTLV/STLV-2, HTLV/STLV-3 (V)	Democratic Republic of the Congo	Ahuka-Mundeke et al. (2011), Van Brussel et al. (1998)
	Zaire Ebolavirus (V)	Cameroon, Gabon	Leroy et al. (2004a, b)
<i>Gorilla gorilla</i> (Western gorilla)	HIV-1/SIVgor (V)	Cameroon	Takehisa et al. (2009)
	HTLV/STLV-1 (V)	Cameroon	Cournaud et al. (2004), Nriren et al. (2004)
	Simian Foamy Virus (V)	Cameroon, Gabon	Wolfe et al. (2004b), Mouinga-Ondémé et al. (2012)
	Rabies (V)	Central African Republic, Kenya	Karugah (1997)
	<i>Strongyloides fulleborni</i> (H)	Central African Republic	Lilly et al. (2002)
	<i>Entamoeba histolytica</i> (P)	Central African Republic	Lilly et al. (2002)
	<i>Balanitium coli</i> (P)	Central African Republic	Lilly et al. (2002)
	<i>Giardia intestinalis</i> (P)	Central African Republic, Rwanda	Sak et al. (2013), Hogan et al. (2014)

Other nonhuman primates					
<i>Colobus angolensis</i> (Angola colobus)	HTLV/STLV-3 (V)	Democratic Republic of the Congo	Ahuka-Mundeke et al. (2012)		
	<i>Strongyloides fulleborni</i> (H)	Uganda	Gillespie et al. (2005)		
<i>Colobus guereza</i> (Mantled guereza)	<i>Entamoeba histolytica</i> (P)	Uganda	Gillespie et al. (2005)		
	<i>Strongyloides fulleborni</i> (H)	Cameroon, Uganda	Gillespie et al. (2005), Pourrut et al. (2011)		
<i>Ptilocolobus badius</i> (Western red colobus)	<i>Entamoeba histolytica</i> (P)	Uganda	Gillespie et al. (2005)		
	HTLV/STLV-1 (V)	Côte d'Ivoire	Leendertz et al. (2010)		
<i>Ptilocolobus tephrosceles</i> (Ugandan red colobus)	HTLV/STLV-1 (V)	Uganda	Goldberg et al. (2009)		
	<i>Strongyloides fulleborni</i> (H)	Uganda	Gillespie et al. (2005)		
<i>Ptilocolobus tholloni</i> (Thollon's red colobus)	<i>Entamoeba histolytica</i> (P)	Uganda	Gillespie et al. (2005)		
	HTLV/STLV-1, HTLV/STLV-3 (V)	Democratic Republic of the Congo	Ahuka-Mundeke et al. (2012).		
<i>Lophocebus albigena</i> (Gray-cheeked mangabey)	HTLV/STLV-1, HTLV/STLV-3 (V)	Cameroon	Liégeois et al. (2012), Locatelli and Peeters (2012)		
	<i>Strongyloides fulleborni</i> (H)	Cameroon	Pourrut et al. (2011)		
<i>Lophocebus aterrimus</i> (Black crested mangabey)	HTLV/STLV-3 (V)	Democratic Republic of the Congo	Ahuka-Mundeke et al. (2012)		
	Zaire Ebolavirus (V)	Cameroon	Leroy et al. (2004b)		
<i>Papio anubis</i> (Olive baboon)	HTLV/STLV-1 (V)	Ethiopia, Kenya	Mahieux et al. (1998), Meertens et al. (2001), Takemura et al. (2002), Locatelli and Peeters (2012)		
	HTLV/STLV-3 (V)	Tanzania	Voevodin et al. (1997)		
<i>Papio cynocephalus</i> (Yellow baboon)	HTLV/STLV-3 (V)	Eritrea, Ethiopia, Senegal	Goubau et al. (1994), Takemura et al. (2002), Meertens and Gessain (2003)		
	HTLV/STLV-1 (V)	South Africa	Mahieux et al. (1998)		
<i>Bacillus anthracis</i> (B)		Namibia	Magwedere et al. (2012)		

(continued)

Table 24.1 (continued)

Bushmeat species	Pathogen	Location	References
<i>Papio</i> sp. (Baboon sp.)	Rabies (V)	Kenya, Namibia, Zambia	Munang'andu (1995), Kamugah (1997), Magwedere et al. (2012)
<i>Theropithecus gelada</i> (Gelada)	HTLV/STLV-3 (V)	Ethiopia	Van Dooren et al. (2004)
<i>Cercocebus agilis</i> (Agile mangabey)	HTLV/STLV-1, HTLV/STLV-3 (V)	Cameroon	Nerrienet et al. (2001), Courgnaud et al. (2004), Liégeois et al. (2008), Sintasath et al. (2009a), Locatelli and Peeters (2012)
	<i>Strongyloides fulleborni</i> (H)	Cameroon	Pourrut et al. (2011)
	<i>Entamoeba histolytica</i> (P)	Central African Republic	Lilly et al. (2002)
	<i>Balantidium coli</i> (P)	Central African Republic	Lilly et al. (2002)
<i>Cercocebus atys</i> (Sooty mangabey)	HIV-2/SIVsm (V)	West Africa	Hirsch et al. (1989), reviewed in Sharp and Hahn (2010), Peeters et al. (2013)
	HTLV/STLV-1 (V)	Sierra Leone	Traina-Dorge et al. (2005)
<i>Cercocebus torquatus</i> (Collared mangabey)	HTLV/STLV-1, HTLV/STLV-3 (V)	Cameroon	Meertens et al. (2001, 2002), Liégeois et al. (2008, 2012)
<i>Mandrillus leucophaeus</i> (Drill)	Zaire Ebolavirus (V)	Cameroon	Leroy et al. (2004b)
<i>Mandrillus sphinx</i> (Mandrill)	Zaire Ebolavirus (V)	Cameroon	Leroy et al. (2004b)
	HTLV/STLV-1 (V)	Cameroon	Nerrienet et al. (2001), Courgnaud et al. (2004), Liégeois et al. (2012)
<i>Allenopithecus nigroviridis</i> (Allen's swamp monkey)	Simian foamy virus (V)	Cameroon, Gabon	Wolfe et al. (2004b), Mouinga-Ondémé et al. (2010)
	HTLV/STLV-1 (V)	Democratic Republic of the Congo	Meertens et al. (2001)
<i>Miopithecus ogouensis</i> (Gabon talapoin)	HTLV/STLV-1 (V)	Cameroon	Courgnaud et al. (2004)
	<i>Strongyloides fulleborni</i> (H)	Cameroon	Pourrut et al. (2011)

<i>Erythrocebus patas</i> (Patas monkey)	HTLV/STLV-1 (V)	Cameroon, Central African Republic, Senegal	Ishikawa et al. (1987), Saksena et al. (1994)
<i>Chlorocebus aethiops</i> (Griwet)	Marburg virus (V)	Uganda	Smith (1982)
<i>Chlorocebus pygerythrus</i> (Vervet monkey)	HTLV/STLV-1 (V)	Ethiopia, Senegal	Meertens et al. (2001), Takemura et al. (2002)
<i>Chlorocebus sabaeus</i> (Green monkey)	HTLV/STLV-1 (V)	Kenya	Meertens et al. (2001)
<i>Chlorocebus tantalus</i> (Tantulus monkey)	<i>Leptospira</i> (B)	Botswana	Jobbins and Alexander (2015)
<i>Cercopithecus albogularis</i> (Sykes' monkey)	HTLV/STLV-1 (V)	Senegal	Meertens et al. (2001), Locatelli and Peeters (2012)
<i>Cercopithecus ascanius</i> (Red-tailed monkey)	HTLV/STLV-1 (V)	Kenya	Meertens et al. (2001), Locatelli and Peeters (2012)
<i>Cercopithecus cephus</i> (Moustached guenon)	HTLV/STLV-1 (V)	Kenya	Mwenda et al. (1999)
<i>Cercopithecus mitis</i> (L'Hoest's monkey)	HTLV/STLV-1 (V)	Democratic Republic of the Congo	Ahuka-Mundeke et al. (2012)
<i>Cercopithecus mona</i> (Mona monkey)	<i>Strongyloides fulleborni</i> (H)	Uganda	Gillespie et al. (2004)
<i>Cercopithecus neglectus</i> (De Brazza's monkey)	HTLV/STLV-1, HTLV/ STLV-3 (V)	Cameroon	Cournaud et al. (2004), Liégeois et al. (2008, 2012), Locatelli and Peeters (2012)
<i>Cercopithecus mitis</i> (Blue monkey)	<i>Strongyloides fulleborni</i> (H)	Cameroon	Pourrut et al. (2011)
<i>Cercopithecus mona</i> (Mona monkey)	<i>Strongyloides fulleborni</i> (H)	Uganda	Gillespie et al. (2004)
<i>Cercopithecus neglectus</i> (De Brazza's monkey)	<i>Strongyloides fulleborni</i> (H)	Kenya, Uganda	Munene et al. (1998), Gillespie et al. (2004)
<i>Cercopithecus mitis</i> (Blue monkey)	HTLV/STLV-1, HTLV/ STLV-3 (V)	Cameroon	Meertens et al. (2001), Sintasath et al. (2009b), Locatelli and Peeters (2012)
<i>Cercopithecus neglectus</i> (De Brazza's monkey)	<i>Strongyloides fulleborni</i> (H)	Cameroon	Pourrut et al. (2011)
<i>Cercopithecus mitis</i> (Blue monkey)	Zaire Ebolavirus (V)	Cameroon	Leroy et al. (2004b)
<i>Cercopithecus neglectus</i> (De Brazza's monkey)	HTLV/STLV-1 (V)	Democratic Republic of the Congo	Ahuka-Mundeke et al. (2012)
<i>Cercopithecus mitis</i> (Blue monkey)	Simian Foamy Virus (V)	Cameroon	Wolfe et al. (2004b)
<i>Cercopithecus neglectus</i> (De Brazza's monkey)	<i>Strongyloides fulleborni</i> (H)	Cameroon	Pourrut et al. (2011)

(continued)

Table 24.1 (continued)

Bushmeat species	Pathogen	Location	References
<i>Cercopithecus nictitans</i> (Greater spot-nosed monkey)	HTLV/STLV-1, HTLV/STLV-3 (V)	Cameroon	Meertens et al. (2001), Courgnaud et al. (2004), Liégeois et al. (2008, 2012), Sintasath et al. (2009b)
<i>Cercopithecus pogonias</i> (Crested mona monkey)	<i>Strongyloides fulleborni</i> (H)	Cameroon	Pourrut et al. (2011)
<i>Cercopithecus wolfi</i> (Wolf's mona monkey)	HTLV/STLV-1 (V)	Cameroon	Courgnaud et al. (2004), Liégeois et al. (2008)
"Vervet monkey"	HTLV/STLV-1 (V)	Democratic Republic of the Congo	Pourrut et al. (2011)
Unspecified primate sp.	Rabies (V)	Zambia	Locatelli and Peeters (2012)
	<i>Strongyloides fulleborni</i> (H)	Uganda	Munang'andu (1995)
	Rabies (V)	Ethiopia, Ghana, Kenya, Malawi, Mozambique; Namibia, Sudan, Uganda, Zimbabwe	Gillespie et al. (2004)
			See summary and discussion in Gautret et al. (2014)
Bats			
<i>Eidolon helvum</i> (African straw-colored fruit bat)	Zaire Ebolavirus (V)	Ghana	Hayman et al. (2010)
	Lagos bat virus (V)	Ghana, Kenya, Nigeria, Senegal	Boulger and Porterfield (1958), Institut Pasteur (1985), Hayman et al. (2008, 2010), Kuzmin et al. (2008)
	Henipaviruses (V)	Cameroon, Ghana, Republic of Congo, Zambia	Hayman et al. (2008), Drexler et al. (2009), Baker et al. (2012), Weiss et al. (2012), Muleya et al. (2014), Pernet et al. (2014)
<i>Hypsignathus monstrosus</i> (Hammer-headed fruit bat)	Marburgvirus (V)	Gabon, Republic of Congo	Pourrut et al. (2009)
	Zaire Ebolavirus (V)	Ghana, Gabon, Republic of Congo	Pourrut et al. (2007, 2009), Hayman et al. (2012)
<i>Epomops franqueti</i> (Franquet's epauletted fruit bat)	Marburgvirus (V)	Gabon, Republic of Congo	Pourrut et al. (2009)
	Zaire Ebolavirus (V)	Ghana, Gabon, Republic of Congo	Pourrut et al. (2007, 2009), Hayman et al. (2012)
<i>Epomophorus gambianus</i> (Gambian epauletted fruit bat)	Zaire Ebolavirus (V)	Ghana	Hayman et al. (2012)

<i>Epomophorus wahlbergi</i> (Wahlberg's epauletted fruit bat)	Lagos Bat Virus (V)	South Africa	Markotter et al. (2006)
<i>Micropteropus pusillus</i> (Peters's lesser epauletted fruit bat)	Marburgvirus (V) Zaire Ebolavirus (V) Lagos Bat Virus (V)	Gabon, Republic of Congo Gabon, Republic of Congo Central African Republic	Pourrut et al. (2009) Pourrut et al. (2009) Sureau et al. (1980)
<i>Rousettus aegyptiacus</i> (Egyptian roussette)	Marburgvirus (V)	Democratic Republic of the Congo, Gabon, Kenya, Republic of Congo, Uganda	Swanepoel et al. (2007), Townner et al. (2007, 2009), Pourrut et al. (2009), Kuzmin et al. (2010b), Amman et al. (2012)
	Zaire Ebolavirus (V)	Gabon, Republic of Congo	Pourrut et al. (2009)
	Lagos Bat Virus (V)	Kenya	Kuzmin et al. (2008)
<i>Myonycteris torquata</i> (Little collared fruit bat)	Zaire Ebolavirus (V)	Gabon, Republic of Congo	Pourrut et al. (2007, 2009)
<i>Nanonycteris veldkampii</i> (Veldkamp's dwarf epauletted fruit bat)	Zaire Ebolavirus (V)	Ghana	Hayman et al. (2012)
<i>Rhinolophus eloquens</i> (Eloquent horseshoe bat)	Marburgvirus (V)	Democratic Republic of the Congo	Swanepoel et al. (2007)
<i>Miniopterus inflatus</i> (Greater long-fingered bat)	Marburgvirus (V)	Democratic Republic of the Congo	Swanepoel et al. (2007)
<i>Miniopterus schreibersii</i> (Schreibers's long-fingered bat)	Duvengahe virus (V)	South Africa	Paweska et al. (2006)
<i>Nycteris gambiensis</i> (Gambian slit-faced bat)	Lagos Bat Virus	Senegal	Institut Pasteur (1985)
<i>Mops condylurus</i> (Angolan free-tailed bat)	Zaire Ebolavirus (V)	Gabon	Pourrut et al. (2009)
Unspecified bat sp.	Duvengahe virus (V)	Kenya	van Thiel et al. (2009)

(continued)

Table 24.1 (continued)

Bushmeat species	Pathogen	Location	References
Rodents			
<i>Funisciurus anerythrus</i> (Thomas's rope squirrel)	Monkeypox virus (V)	Democratic Republic of the Congo	Khodakevich et al. (1986)
<i>Funisciurus</i> sp. (African striped squirrel sp.)	Monkeypox virus (V)	Ghana	Reynolds et al. (2010)
<i>Heliosciurus gambianus</i> (Gambian sun squirrel)	Monkeypox virus (V)	Ghana	Reynolds et al. (2010)
<i>Paraxerus cepapi</i> (Smith's bush squirrel)	<i>Leptospira</i> (B)	Botswana	Jobbins and Alexander (2015)
<i>Xerus</i> sp. (African ground squirrel sp.)	Monkeypox virus (V)	Ghana	Reynolds et al. (2010)
Unspecified squirrel sp.	Rabies (V)	Namibia, Zimbabwe	Pfukenyi et al. (2009), Magwedere et al. (2012)
<i>Lophuromys sikapusi</i> (Rusty-bellied brush-furred rat)	Mokola virus (V)	Central African Republic	Saluzzo et al. (1984)
<i>Mastomys natalensis</i> (Natal mastomys)	Lassa Fever (V)	Guinea	Ter Meulen et al. (1996)
<i>Rattus norvegicus</i> (Brown rat)	<i>Leptospira</i> (B)	Botswana	Jobbins and Alexander (2015)
Unspecified "rat species"	Rabies (V)	Namibia	Magwedere et al. (2012)
<i>Cricetomys</i> sp. (Giant pouched rat sp.)	Monkeypox virus (V)	Ghana	Reynolds et al. (2010)
<i>Atherurus africanus</i> (African brush-tailed porcupine)	Salmonella (B)	Gabon	Bachand et al. (2012)
Aardvark			
<i>Orycteropus afer</i> (Aardvark)	<i>Leptospira</i> (B)	Botswana	Jobbins and Alexander (2015)

Ungulates				
<i>Equus burchellii</i> (Burchell's zebra)	<i>Bacillus anthracis</i> (B)	Namibia	Magwedere et al. (2012)	
<i>Phacochoerus aethiopicus</i> (Desert warthog)	Rabies (V)	Namibia	Magwedere et al. (2012)	
<i>Phacochoerus africanus</i> (Common warthog)	<i>Leptospira</i> (B)	Botswana	Jobbins and Alexander (2015)	
<i>Alcelaphus buselaphus</i> (Hartebeest)	Rabies (V)	Namibia	Magwedere et al. (2012)	
<i>Connochaetes taurinus</i> (Blue wildebeest)	<i>Bacillus anthracis</i> (B)	Namibia	Magwedere et al. (2012)	
<i>Antidorcas marsupialis</i> (Springbok)	<i>Bacillus anthracis</i> (B)	Namibia, Tanzania	Lembo et al. (2011), Magwedere et al. (2012)	
<i>Syncerus caffer</i> (African buffalo)	<i>Bacillus anthracis</i> (B)	Namibia	Magwedere et al. (2012)	
<i>Taurotragus oryx</i> (Common eland)	<i>Brucella</i> (B)	Namibia	Magwedere et al. (2011)	
<i>Tragelaphus strepsiceros</i> (Greater kudu)	<i>Bacillus anthracis</i> (B)	Tanzania	Lembo et al. (2011)	
<i>Cephalophus</i> sp. (Duiker sp.)	<i>Brucella</i> (B)	Botswana, Mozambique	Alexander et al. (2012), Tanner et al. (2014)	
<i>Sylvicapra grimmia</i> (Bush duiker)	Rabies (V)	Namibia, Zimbabwe	Pfukenyi et al. (2009), Magwedere et al. (2012)	
<i>Hippotragus niger</i> (Sable antelope)	<i>Bacillus anthracis</i> (B)	Namibia	Magwedere et al. (2012)	
<i>Oryx gazelle</i> (Gemsbok)	Rabies (V)	Namibia	Magwedere et al. (2012)	
Unspecified "oryx," "antelope," "duiker"	Rabies (V)	Namibia	Magwedere et al. (2012)	
<i>Virus, H</i> helminth, <i>P</i> protozoan, <i>B</i> bacteria	Zaire Ebolavirus (V)	Gabon	Leroy et al. (2004a)	
	Rabies (V)	Zimbabwe	Pfukenyi et al. (2009)	
	Rabies (V)	Zimbabwe	Pfukenyi et al. (2009)	
	Rabies (V)	Namibia	Magwedere et al. (2012)	
	Rabies (V)	Namibia	Magwedere et al. (2012)	

Virus, H helminth, *P* protozoan, *B* bacteria

*See text for further discussions of pathogens in great apes, including uncertainty as to whether apes or humans are the source of spillovers

Viral Pathogens

Viruses are obligatory intracellular parasites characterized primarily by the nature of their nucleic acids (DNA or RNA; single or double stranded, etc.). They are the most abundant form of life on earth; many viruses are recognized as important disease-causing agents, and they are subject to frequent mutation and thus evolution. The advent of modern molecular techniques has advanced our understanding of viral diversity and pathogenesis in both animal and human hosts. For example, in relation to bushmeat, it is now clear that many virus variants are present in hunted nonhuman primate species, which have received most of the research attention, and that these variants have crossed between nonhuman primates and humans on multiple occasions (Peeters and Delaporte 2012; Table 24.1). Bats and rodents are also major zoonotic virus carriers (Meerburg et al. 2009; Baker et al. 2013); other taxonomic groups are less studied, at least in sub-Saharan Africa. Several sub-Saharan African viruses of importance are vector-borne, including Rift Valley Fever and Crimean-Congo hemorrhagic fever. While one presumes that this would make them unlikely to spread via bushmeat-related activities, the possibility remains that animal handling could present a risk (Magwedere et al. 2012). However, no significant links between vector-borne viruses and bushmeat hunting have been made, and we will not include a discussion of these viruses here.

HIV/SIV: The most notable virus to emerge from the bushmeat interface is human immunodeficiency virus (HIV). While the origin of HIV was long obscured, Human HIV-1 and HIV-2 are believed to have evolved from strains of simian immunodeficiency virus (SIV) (Hahn et al. 2000; Lemey et al. 2003; Van Heuverswyn and Peeters 2007; Sharp and Hahn 2010; Peeters and Delaporte 2012; Peeters et al. 2013; Kazanji et al. 2015). Evidence suggests that SIV crossed over to humans by blood contact when hunters had an exposed open wound or injured themselves during the butchering of nonhuman primates (Hahn et al. 2000; Wolfe et al. 2004a, b; Karesh and Noble 2009). The closest relatives of HIV-1 found among nonhuman primates are SIVcpz and SIVgor, from common chimpanzees and western gorillas in west central Africa (Gao et al. 1999; Sharp et al. 2005; Keele et al. 2006; Van Heuverswyn et al. 2006, 2007; Takehisa et al. 2009) and at least four separate spillovers have occurred (Peeters et al. 2013). HIV-2 is derived from SIVsmm from sooty mangabeys (*Cercocebus atys*) in West Africa (Apetrei et al. 2005; Hirsch et al. 1989; Gao et al. 1992; Ayouba et al. 2013), where high viral genetic diversity exists and where transmission is believed to have occurred at least eight times.

The potential for future and continued spillovers from SIVs is high, and multiple species-specific variants exist. For example, Peeters et al. (2002) and Peeters (2004) estimated that more than 20 % of nonhuman primates hunted for food are infected with a variant of SIV; Locatelli and Peeters (2012) and Peeters et al. (2013) noted that at least 45 species-specific variants of SIV from at least 45 primate species are currently recognized. Aghokeng et al. (2010) sampled 1856 nonhuman primate carcasses from 11 species found in bushmeat markets in Cameroon. They documented low overall prevalence of SIV (only 2.93 % of carcasses), with the lowest prevalence

found among the most common species in the market. However, they did find SIV variants in about 70 % of the tested primate species. In total, serological evidence of SIV infection has been documented for at least 40 different primate species (Aghokeng et al. 2010; Liégeois et al. 2011, 2012). Cross-species transmission of strains and co-infection with more than one strain have been documented, sometimes followed by genetic recombination (Hahn et al. 2000; Bibollet-Ruche et al. 2004; Aghokeng et al. 2007; Gogarten et al. 2014), a recipe for future spillovers into humans (Locatelli and Peeters 2012).

Human T-Cell Lymphotropic Virus (HTLV): Similar to HIV, human T-lymphotropic viruses (HTLV) are related to simian viral lineages in which significant diversity has been found (Ahuka-Mundeke et al. 2012; Peeters and Delaporte 2012). All three sub-Saharan great apes and 30 additional nonhuman primates have been documented to have STLV/HTLV variants and a variety of HTLV viruses have been documented in wildlife and in central African hunters (Calattini et al. 2009, 2011; Cournaud et al. 2004; Sintasath et al. 2009a, b; Wolfe et al. 2005b; Zheng et al. 2010; Locatelli and Peeters 2012). Similar to HIV/SIV, dual infections with more than one variant have been documented in nonhuman primates (Agile mangabeys, *Cercocebus agilis*; Cournaud et al. 2004) and in humans (Calattini et al. 2011; Wolfe et al. 2005b).

Simian Foamy Virus: Simian foamy retroviruses (SFV) are endemic in most African primates (Hussain et al. 2003; Switzer et al. 2005; Peeters and Delaporte 2012) and are known to transmit to humans (Sandstrom et al. 2000; Switzer et al. 2004; Calattini et al. 2007; Mouinga-Ondémé et al. 2010, 2012). Like the other retroviruses discussed above (HIV and HTLV), SFV is genetically diverse and relatively host species-specific. In Cameroon, Wolfe et al. (2004b) documented three geographically independent SFV infections, which could be traced to De Brazza's monkey (*Cercopithecus neglectus*), mandrill (*Mandrillus sphinx*), and western gorilla. Likewise, in Gabon, Mouinga-Ondémé et al. (2010, 2012) documented human spillover events involving multiple strains of SFV, with infected humans having been bitten by common chimpanzees, western gorillas, or mandrills infected with their respective variant of SFV.

Ebola and Marburg Viruses: There are seven species of filoviruses currently identified, five of which occur in sub-Saharan Africa—Genus *Ebolavirus*: Tai forest ebolavirus (TAFV), Sudan ebolavirus (SUDV), Zaire ebolavirus (EBOV), Bundibugyo virus (BDBV); Genus *Marburgvirus*: Marburg virus (MARV). These pathogens are periodically emerging viruses, typically from single spillover events, which cause hemorrhagic fevers (reviewed by Olival and Hayman 2014; Rougeron et al. 2015 (but note that Rougeron's listing for a single case of SUDV in Sudan in 2011 is erroneous)). The 2014–2015 West Africa outbreak of EBOV is still ongoing at the time of this writing (Labouba and Leroy 2015). While the zoonotic source of this outbreak is unknown, three initial outbreaks of the Ebola virus in the Democratic Republic of the Congo from 1976 to 1979 involved victims who were reported to have handled western gorilla or common chimpanzee carcasses or to have had physical contact with people who touched the animals (Leroy et al. 2004a, b). Similarly,

Marburgvirus was first identified in laboratory workers who had dissected imported grivet (*Chlorocebus aethiops*) (Martini et al. 1968; Siegert et al. 1968). Both western gorillas and common chimpanzees have suffered significant mortality from filovirus outbreaks (Walsh et al. 2003; Leroy et al. 2004a, b; Bermejo et al. 2006; Rizkalla et al. 2007) and antibodies to EBOV were documented in several other primate species by Leroy et al. (2004b). The single case of TAFV occurred in an ethnologist likely infected while performing a necropsy of a dead common chimpanzee following a rash of common chimpanzee deaths in the Tai National Park in Côte d'Ivoire (Le Guenno et al. 1995; Wyers et al. 1999). Beyond primates, other incidental hosts in the wild are possible, as was demonstrated for duikers (*Cephalophus* spp.) (Leroy et al. 2004a; Rouquet et al. 2005). As reviewed by Weingartl et al. (2013), both dogs (naturally) and pigs (at least experimentally) can also be infected. During the 2001–2002 EBOV outbreak in Gabon, Allela et al. (2005) found over 30 % seroprevalence in dogs living in villages with EBOV human and animal cases. Those dogs appeared to be asymptomatic and were presumed to be exposed by scavenging wild animals.

Although incidental hosts likely play important roles in the ecology of these viruses, especially when moribund or dead animals are consumed, strong evidence suggests that bats are the natural reservoir hosts for at least Marburgvirus and EBOV. For Marburgvirus, the cave dwelling and densely packed Egyptian rousette fruit bat (*Rousettus aegyptiacus*) is now well-documented as a reservoir host (Towner et al. 2009; Amman et al. 2012), but antibodies against the virus and/or the presence of viral RNA have been found in several other species (see Table 24.1). The strong association of Marburgvirus with the Egyptian rousette makes sense in light of the outbreaks of this virus in people visiting tourist caves or working in mines (Adjemian et al. 2011; Timen et al. 2009; Towner et al. 2009; Amman et al. 2012). The picture for EBOV is less clear, but evidence of infection has been found in at least eight sub-Saharan bat species (Pourrut et al. 2007, 2009; Hayman et al. 2010, 2012; Table 24.1). Of the ten bat species listed in Table 24.1 for Marburgvirus and EBOV, seven are fruit bats, which are relatively larger and more visible, and thus targets of bushmeat hunters. That said, bushmeat hunting of these bats is not ubiquitous throughout their range and cannot solely explain filovirus spillovers. Mari Saéz et al. (2015) unconvincingly suggested the non-fruit bat, *Mops condylurus*, might have been the source of the 2014–2015 West African Ebola outbreak. Pourrut et al. (2009) found evidence of antibodies against ZEBOV in this species, but there is no real evidence that this free-tailed bat played a role in the 2014–2015 outbreak. To date, no bat host has been identified for BDBV, SUDV, or TAFV and broader surveillance for indications of these viruses in bats and other hosts should be conducted.

Henipaviruses and Other Paramyxoviruses: Hendra virus and Nipah virus (HNVs) are paramyxoviruses in the genus *Henipavirus* that emerged in Australia and south-east Asia, respectively, with fruit bats in the genus *Pteropus* (family Pteropodidae) as reservoir hosts (reviewed by Croser and Marsh 2013). However, recent studies have identified *Henipavirus* and Henipa-like viruses in sub-Saharan African fruit bats, which are a phylogenetically distinct clade of pteropodid bats that do not overlap distributionally with any *Pteropus* species. Documentation of *Henipavirus* and

related RNA (Drexler et al. 2009; Muleya et al. 2014; Baker et al. 2012) and anti-*Henipavirus* antibodies (Hayman et al. 2008; Pernet et al. 2014) in the African straw-colored fruit bat (*Eidolon helvum*) clearly show that this deadly and diverse viral group is present in sub-Saharan Africa. This bat species is a frequent target of hunters and a significant protein source where it is found (Kamins et al. 2011b). Weiss et al. (2012) documented the presence of this group of viruses in these bats found live in bushmeat markets. Strong evidence of spillover to humans was documented by Pernet et al. (2014) who found antibodies against HNVs in human samples from Cameroon. These seropositive human samples were found almost exclusively in individuals who reported butchering these bats. This bat is also a long-distance migrator with significant panmixia across the continent, which could facilitate viral transmission between bats (Peel et al. 2013).

The paramyxovirus story in sub-Saharan Africa is still unfolding. Both Drexler et al. (2012) and Baker et al. (2012) describe great diversity in paramyxoviruses from sub-Saharan bats. In their comprehensive study of the evolutionary history of this virus family, Drexler et al. (2012) found that the *Henipavirus* lineage originated in Africa and identified bats as the likely origin of this large family of viruses. A precautionary tale from sub-Saharan Africa comes from the recent discovery and naming of the Sosuga virus from a wildlife researcher who became very ill after handling and dissecting hundreds of bats and rodents in Uganda and South Sudan (Albariño et al. 2014). This virus is most closely related to Tuhoko virus 3, a rubula-like virus recently isolated from the Leschenault's Rousette fruit bat (*Rousettus leschenaultii*) in southern China. Amman et al. (2015) subsequently found Sosuga virus in *R. aegyptiacus* captured from multiple locations in Uganda; the researcher infected by this virus handled this species extensively in her studies.

Rabies and Other Lyssaviruses: Rabies is the oldest known zoonotic EID, recorded as early as the twenty-third century BC (Steele and Fernandez 1991). An estimated 25,000 people die in Africa each year from rabies (Dodet et al. 2015), some portion of which may be from exposure that occurs in bushmeat-related activities, although most human cases can be attributed to domestic dogs. Rabies virus (RABV) is in the *Lyssavirus* genus. It is joined in Africa by at least five additional species: Lagos bat virus (LBV), Mokola virus (MOKV), Duvenhage virus (DUVV), Shimoni bat virus (SHIBV), and the newly proposed Ikoma lyssavirus (IKOV). These viruses have bat(s) as their reservoir host (Banyard et al. 2014) with two exceptions. The Mokola virus is found in shrews (*Crocidura* spp.), rusty-bellied brush-furred rat (*Lophuromys sikapusi*; Saluzzo et al. 1984), and companion animals (Delmas et al. 2008; Kgaladi et al. 2013). The Ikoma virus has thus far only been documented in African civets (*Civettictis civetta*; Table 24.1, Marston et al. 2012). A variety of wildlife species can be secondary hosts of rabies (e.g., in Botswana, see Moagabo et al. 2009) and rabies has been documented to occur in a number of nonhuman primate species, including those encountered in the bushmeat trade (Gautret et al. 2014). Lyssaviruses are found worldwide, but the greatest genetic diversity is in Africa and Lagos bat virus may be more than one species (Delmas et al. 2008; Markotter et al. 2008; Kuzmin et al. 2010a). While most human cases are due to rabies virus, Duvenhage virus has been documented in human fatalities associated with bat scratches that likely transmitted the virus

(van Thiel et al. 2009; Paweska et al. 2006). Mokolo virus has been detected in two human cases without mortality (Kgaladi et al. 2013).

The lyssavirus story in Africa will continue to emerge due to increased surveillance and improved molecular techniques. The 2012 discovery of Ikoma virus in an African civet in Serengeti National Park in Tanzania, where domestic dogs are largely absent and detection in bat hosts is nonexistent (Marston et al. 2012; Horton et al. 2014), highlights the likelihood that many more lyssaviruses exist in a variety of host species. The true diversity of lyssaviruses in Africa, and the potential for human spillover via bushmeat-related activities, remains to be discovered.

Lassa and Other Arenaviruses: Arenaviruses include a number of zoonotic species, typically transmitted from rodents to humans. Lassa virus is the best known of the viral hemorrhagic arenaviruses in Africa and is well-documented in West Africa, especially Guinea, Sierra Leone, Nigeria, and Liberia. As with some of the bacterial pathogens described below, the primary risk comes from peridomestic exposure to the rodent host, the natal mastomys (*Mastomys natalensis*), via exposure to urine or fecal materials. However, Ter Meulen et al. (1996) found a strong association between hunting of peridomestic rodents and antibodies to and symptoms of Lassa virus, tying bushmeat-related activities to the spillover of this virus to humans.

Human Monkeypox Virus: Contrary to its moniker, the reservoir hosts of human monkeypox virus (MPX) are neither monkeys nor humans, but rather rodents. The first case of human monkeypox was identified in 1970 in the Democratic Republic of the Congo, with subsequent outbreaks in Liberia, Sierra Leone, Côte d'Ivoire, Nigeria, and Democratic Republic of the Congo (reviewed by Reynolds et al. 2010; Rimoin et al. 2010). Recent MPX increases in the Democratic Republic of the Congo and elsewhere have been attributed to cessation of the human smallpox vaccine, which conferred some immunity to other pox viruses (Rimoin et al. 2010). Human and nonhuman primate infections are suspected to result from wildlife exposure such as would occur in bushmeat-related activities; infected species include squirrels (e.g., Thomas's rope squirrel, *Funisciurus anerythrus*; Khodakevich et al. 1986; African ground squirrels; *Xerus* sp.; Reynolds et al. 2010), dormice (*Graphiurus* sp.; Reynolds et al. 2010), and giant pouched rats (*Cricetomys* sp.; Reynolds et al. 2010). The outbreak that occurred in the USA in 2007 after exposure to rodents in the illegal pet trade also linked human monkeypox to rope squirrels, dormice, and pouched rats (Hutson et al. 2007). While dormice are small and not likely to be the target of hunting, the diurnal and highly visible squirrels and the giant pouched rats are routinely hunted (Taylor et al. 2015), making the spillover to humans highly plausible.

Bacteria

Jones et al. (2008) list 54.3 % of EID events as being caused by bacteria and there is good evidence to suggest that bacterial pathogens have the potential to be just as important as viruses when it comes to those that may spillover due to

bushmeat-related activities, but in this capacity they have received far less attention (Cantas and Suer 2014). Transmission pathways for bacterial pathogens can occur through direct exposure to body fluids or feces, but they can also possibly be transferred indirectly through exposure to disease vectors such as fleas and ticks when handling animals. In a rare survey of bacterial pathogens that might spillover via bushmeat-related activities, Bachand et al. (2012) sampled muscle from 128 bushmeat carcasses from multiple species at markets in Gabon for the presence of *Campylobacter*, *Salmonella*, and *Shigella*. While they only recorded the presence of *Salmonella*, the potential for contamination and thus spillover of enteric pathogens from carcass handling remains high, especially in the days after purchase when pathogens continue to replicate. Bacteria in the genus *Leptospira* are endemic sub-Saharan African pathogens that have a high risk of spillover during bushmeat-related activities as they are shed in urine. Jobbins and Alexander (2015) documented their widespread presence in wild mammals, birds, and reptiles, highlighting the role that wildlife may play in leptospirosis. The bushmeat interface may also play a role in human cases of anthrax, caused by *Bacillus anthracis*, which is largely a disease of grazing herbivorous mammals, but to which common chimpanzees are also susceptible (Leendertz et al. 2004). If bushmeat includes not only the hunting of apparently healthy animals but also sick animals or salvage of contaminated carcasses, the risk of human outbreaks increases (Hang'ombe et al. 2012).

A number of bacterial pathogens are vector-borne, which at face value would make them unlikely to spread via bushmeat-related activities. However, especially for bacteria with flea or tick as vectors, as opposed to mosquitoes for example, one can envision that animal handling could present a risk. The most frightening among the vector-borne bacterial pathogens is plague, caused by the bacteria *Yersinia pestis* and transmitted through the infected fleas of rodents. Africa remains an endemic region of importance for this pathogen (World Health Organization 2005; Davis et al. 2006). Fleas and ticks are also responsible for transmitting rickettsial pathogens, such as *Rickettsia africae*, which causes African tick-bite fever (ATBF). Mediannikov et al. (2012) collected ticks from duikers and a pangolin that were living in close proximity to humans in Guinea and found *R. africae* in 10 % of ticks collected from the tree pangolin (*Manis tricuspis*), suggesting the potential for spillover with the close handling of these animals. Further research is clearly and urgently needed to fully assess the potential for bacterial disease spillovers via bushmeat-related activities.

Helminths

The helminths or “worm-like” animals include many parasites of zoonotic potential, although Taylor et al. (2001) found helminthes less likely to cause EIDs. Humans engaging in bushmeat-related activities are likely exposed to these pathogens via exposure to fecal material in which eggs are shed, from transcutaneous exposure to infectious larvae, or from consumption of uncooked meat (McCarthy and Moore 2000).

Several studies have examined the prevalence of helminths in animals from bushmeat markets and found high rates of multiple species. For example, Adejinmi and Emikpe (2011) collected fecal samples from greater cane rats (*Thryonomys swinderianus*) and bush duikers (*Sylvicapra grimmia*) in bushmeat markets in Nigeria and documented high prevalence rates (83.3 % and 53.8 %, respectively) of helminth ova in feces as well as larvae from fecal cultures. Likewise, Magwedere et al. (2012) and Mukaratirwa et al. (2013) reviewed the evidence for *Trichinella* infection in humans, livestock, and wildlife in sub-Saharan Africa and noted that bush-pigs (*Potamochoerus* spp.) and desert warthogs (*Phacochoerus aethiopicus*) are a source for human infection. As is the case with many other pathogens, humans and nonhuman primates share susceptibility to many parasitic helminth species (Pedersen et al. 2005; Pourrut et al. 2011). Pourrut et al. (2011) sampled gastrointestinal parasites from 78 wild monkeys of 9 species collected from bushmeat markets in Cameroon and documented high helminth loads, including species known to infect humans. Gillespie et al. (2010) had similar findings from common chimpanzee fecal samples. Overall, the available evidence suggests that spillover of many of these pathogens during bushmeat-related activities is likely.

Protozoan

Protozoans are a paraphyletic group of eukaryotic organisms that are neither animals, plants, nor fungi and include amoebas and giardia. The risk of protozoan spillover from bushmeat-related activities is similar to that for helminths and bacteria in that exposure to feces, bodily fluids, and even potentially to meat could transmit disease to a permissive human host (Pourrut et al. 2011). A number of protozoans are important pathogens with zoonotic potential (Taylor et al. 2001). Perhaps the best example are the amoebozoa, which cause diarrheal disease and which are documented in a variety of animals, including bushmeat species such as nonhuman primates (Gillespie et al. 2010; Pourrut et al. 2011). Gillespie et al. (2010) documented the amoeba *Entamoeba histolytica* and the ciliated protozoan *Balantidium coli* in common chimpanzees; both are human pathogens (although the direction of spillover is uncertain, as common chimpanzees and other primates may have obtained this parasite from humans). Indeed, Lilly et al. (2002) documented both protozoans in common chimpanzees, western gorillas, agile mangabeys, and humans living in the same region in Central African Republic. A number of other nonhuman primates have had documented *E. histolytica* infections as well (see Table 24.1). Other protozoan examples include *Toxoplasma gondii*, which causes the disease toxoplasmosis, but could not be detected during a recent, albeit small scale, survey of bushmeat (Prangé et al. 2009) and water/foodborne parasites such as *Giardia*. Recent studies have documented *Giardia* in a variety of species that exist in the bushmeat trade, including western gorilla and African buffalo (*Syncerus caffer*) (Hogan et al. 2014).

Fungi

Fungi are increasingly being recognized as important pathogens that may emerge, even in humans (Jones et al. 2008; Fisher et al. 2012), and a number of fungi are considered medically important. In particular, fungal infections are problematic for people who are immunosuppressed (e.g., from HIV infection), in which case their immune systems are unable to adequately fight the infection. Nonetheless, we have uncovered no examples of EIDs in Africa caused by fungal pathogens not related to human immunosuppression, as even the 1950s outbreak of cryptococcal meningitis in the Democratic Republic of the Congo has been likely linked to co-infection by HIV (Molez 1998; Jones et al. 2008).

Prions

Only 5 % of prion diseases are acquired (as opposed to inherited), but these include the well-publicized outbreaks of scrapie, bovine spongiform encephalopathy (BSE, or “mad cow disease”), and chronic wasting disease (CWD) in ungulates from Europe and North America. Of these, only BSE has been detected in humans and in captive-held primates (Imran and Mahmood 2011a, b; Bons et al. 1999; Lee et al. 2013), likely due to consumption of contaminated meat products. The authors have found no descriptions of infectious prion diseases in Africa, but this poorly studied pathogen type may well be present in the world’s second largest continent. As it relates to bushmeat-related practices, prions can be found in nearly all tissues and are resistant to degradation, even by cooking, rendering them a potential pathogen worth watching.

Local Knowledge and Perception of Disease Risk

The risk of disease spillover from bushmeat to hunters is highest during butchering and especially if no precautions are taken. Whether hunters take precautions may depend on their knowledge and perception of disease risk. There is increasing evidence that the perception of and knowledge about zoonotic diseases is generally low but varies strongly between sites. A survey among rural bushmeat hunters and traders in Sierra Leone showed that 24 % reported knowledge of disease transmission from animals to humans (Subramanian 2012). Similarly, 23 % of rural–urban hunters and traders in Ghana perceived a disease risk from a bat-bushmeat activity, with significantly more respondents associating risk with bat consumption than bat preparation or hunting (Kamins et al. 2014). Individuals who participate in butchering wild animals typically associate less risk to meat preparation and consumption than those who do not participate in butchering (Kamins et al. 2014) (Fig. 24.2).

Fig. 24.2 A pangolin being prepared in rural Ghana; photo credit Laura Kurpiers



LeBreton et al. (2006) found that hunters and butchers who perceived personal risks were significantly less likely to butcher wild animals, but that risk perception was not associated with hunting and eating bushmeat. Thirty-three percent of bushmeat consumers in a Ghanaian market were not aware that zoonotic diseases could be transmitted from bushmeat to humans. Those who were aware gave Ebola (48 %) and anthrax (16 %) as examples of zoonotic diseases (Kuukyi et al. 2014). In contrast, a large-scale survey among rural Central African population showed that the majority (74 %) of respondents perceived contact with bushmeat blood or body fluids as dangerous (LeBreton et al. 2006). Unfortunately, studies in this field can be challenging, as reported perceptions may differ from actual or ‘revealed’ behaviors and beliefs (Wilkie 2006).

Although there seems to be some level of risk awareness in certain human populations, several studies report a distinct lack of precautionary behavior, resulting in hunters, butchers, and consumers exposing themselves to zoonotic diseases. LeBreton et al. (2006) found that only 4 % of hunters and 2 % of people reporting butchering indicated that they took precautions against contact with animal blood and fluids while hunting and butchering. Furthermore, the few that took precautions may not have protected themselves adequately, as the most common response was “generally being careful.” This was followed by “washing hands,” and the least number of participants reporting “avoiding contact with blood, draining blood from carcasses and wearing suitable clothing.” Paige et al. (2014) examined human–animal

interactions in western Uganda and found that nearly 20 % of participants reported either being injured by an animal or having contact with a primate. The most commonly reported animal injuries were bites (72.9 %) and scratches (23.2 %). In a separate study, it was also shown that although Ghanaian hunters generally handle live bats, they do not typically use protective measures such as gloves, and thereby come into contact with blood through scratches and bites (Kamins et al. 2014). Given the lack of awareness and precautionary measures taken among people who come into contact with bushmeat, the opportunity for new zoonotic pathogens to spillover into humans remains high (LeBreton et al. 2006). This is especially true, since the current rate of hunting wild animals will likely continue—at least until domestic animal production increases and can support the protein needs of the local people.

The Way Forward

Current global disease control efforts focus almost exclusively on responding long after a spillover event has occurred, which increases the risk of a single spillover event causing an epidemic or pandemic. This retroactive response to emerging disease outbreaks is often costly economically and in terms of human well-being (Childs and Gordon 2009; United Nations Development Program 2015). Increased pre-spillover surveillance measures along with quantification of spillover risk is critically needed. For example, Wolfe et al. (2004b, 2005b) found that 1 % of rural Cameroonians are infected with wild primate variants of T-lymphotropic viruses and another 1 % are infected with wild primate variants of simian foamy virus. These sorts of data are simply lacking for most emergent disease systems. Here we will discuss the regulatory and educational measures that could be taken to mitigate the risk of a zoonotic spillover event and spread. Such efforts should be undertaken as a part of a comprehensive response to other sub-Saharan public health crises so as to not divert scarce resources. For example, increases in EID surveillance efforts and in post-emergence management go hand in hand with the improved healthcare infrastructure that must become a priority for sub-Saharan Africa.

At face value, the risk of disease transmission would be reduced if people stopped harvesting bushmeat; however, this scenario is not realistic given the importance of bushmeat in many communities in Africa for which there is limited affordable access to alternate protein sources (Pike et al. 2010; Gebreyes et al. 2014). A more practical option may be to restrict hunting of nonhuman primates, as many zoonotic EIDs have come from them, and instead allow communities to hunt smaller-bodied mammals with higher reproductive rates. Any intervention aiming to restrict access to wildlife should involve community leaders and stakeholders during public outreach to reduce the risk of alienating communities (Monroe and Willcox 2006). The education and enforcement necessary to implement such a restriction must consider the cultural and economic contexts surrounding individual communities. Consider, for example, the problems with enforcement of access restrictions and the

history of antagonistic relationships due to exclusion from protected areas between conservationists and local communities. Without proper educational outreach, this could result in backlash from local communities. Furthermore, using zoonotic diseases to enforce hunting restrictions runs the risk of demonizing species considered to be the main disease carriers. Nonhuman primates could then become targets and their populations could be decimated (Pooley et al. 2015).

A more realistic strategy may be to concentrate on preventing future zoonotic spillover events through culturally appropriate education and preventing the spread of diseases through better disease surveillance. In that effort, it would also be important to incorporate collaborative and interdisciplinary approaches between veterinary researchers, ecologists, microbiologists, public health researchers, and anthropologists to develop surveillance and research approaches that will be both culturally appropriate and improve detection of zoonotic diseases tied to bushmeat hunting (Kilonzo et al. 2014).

Education

The risk of disease transmission could be reduced through community education that focuses on people with high levels of exposure to wild animals (Wolfe et al. 2007). Communicating with hunters and butchers about the risks associated with bushmeat and promoting awareness of safer techniques may reduce current levels of pathogen exposure and transmission. To enhance the effectiveness of prevention campaigns, it is particularly important to reinforce the potential for infections during hunting and butchering as this may be overlooked by some hunters (LeBreton et al. 2006). Because the risk perception of hunters and those engaging in butchering wild animals has a negative association with the level of participation in meat preparation and consumption (Kamins et al. 2014), this may reduce current levels of pathogen exposure and transmission, if not by discouraging individuals to participate in preparation and consumption, then by encouraging those individuals to more proactively consider safety and preventative measures.

Global Viral Forecasting (GVF; now “Global Viral” and “Metabiota”) has been pivotal in educating vulnerable populations in rural central Africa by providing information on the risk of zoonotic disease transmission from hunting wild animals (LeBreton et al. 2012). Hunters are informed about disease risks associated with different species, what steps can be taken to avoid infections, and how they can reduce their contact with blood and body fluids of wild animals. Hunters are urged to redirect hunting efforts away from apes and monkeys and towards less risky species such as antelope and rodents, while also being discouraged from butchering animals when there are cuts or injuries on their hands and limbs.

Of course, a common aspect of such attempts at social outreach and education is that even when it is possible to promote awareness, individuals may not believe the hazard is important or that it could affect them. Some authors have even found that when people do believe the risk is real and relevant, there is often little evidence that

this knowledge promotes a change in behavior (McCaffrey 2004). For example, a pilot education program among Ghanaian hunters resulted in substantially improved understanding of disease risk, yet largely failed to change peoples' behavior (Kamins et al. 2014). When asked about what would change their behavior, participants responded; becoming ill from zoonotic disease followed by alternative livelihoods and stricter laws. Because awareness is not directly related to behavior, Monroe and Willcox (2006) suggest that campaigns should not rely on the threat of infection to change behavior, but should rather use community leaders to change cultural norms associated with hunting and educate people involved in butchering about best practices of how to protect themselves.

Surveillance

With the increasing prevalence of zoonotic disease emergence and the associated risk for public health, we have to improve our understanding of the dynamics of spillover events of pathogens from animal to human hosts (Rostal et al. 2012) and improve systematic global monitoring efforts. This could help detect, define, and control local human emergence while it is still locally confined and before it has a chance to spread globally. Improved detection and surveillance will lead to a better prioritization of public health efforts. One of the most effective strategies in terms of early detection of an emergent pathogenic threat would be to focus surveillance efforts among people who are highly exposed to at-risk animals and on the animal populations to which they are exposed (LeBreton et al. 2012). Bushmeat hunters would be an important target group, as they are in contact with bodily fluids from animals and are at risk for transmission and infection from novel pathogens.

As an example, GVF has established monitoring programs at multiple sites throughout Central Africa to detect the moment of a pathogen spillover, which can then be used to predict and ultimately prevent zoonotic disease emergences (Evans and Wolfe 2013). In order to track and provide data for EIDs, this effort coordinates the collection of filter-paper blood samples from both hunted animals and people who hunt and butcher wild animals. Early results have shown that this type of surveillance can assist in early detection of new diseases by offering insight into pathogen origin. It would also help describe the spillover dynamics of new or existing diseases. Such data are valuable for developing a detailed, mechanistic understanding of the processes that drive disease emergence and prevent spillovers from spreading in early stages of an outbreak. Contextualizing the relative or actual risks of spillovers would be vital for the preferential allocation of resources to high-risk regions or humans who perform high-risk activities (Daszak et al. 2007). As part of these efforts, improved knowledge of how anthropogenic environmental changes and sociological or demographic factors affect the risk of disease emergence will likely be a cost-effective and sustainable mechanism to reduce or control disease spillover risks (Daszak et al. 2007).

Call for Research

The social and environmental issues surrounding bushmeat represent a complex problem for conservation, global public health, and sustainable development, as it is often the poorest and most vulnerable populations who depend on bushmeat for income or food security. Accordingly, the challenge should be addressed in a holistic manner, by integrating multiple efforts to achieve common objectives. Although much progress has been made not only in addressing the problems concerning bushmeat harvest and zoonotic disease spillover, there is much work to be done. Research that would pave the way for future efforts would include the quantification of social response to environmental policy change (e.g., in the context of harvest restriction), development of a more representative picture of bushmeat consumption in Africa, a broader exploration of the many classes of pathogens within wildlife, and more thorough understanding and quantification of the dynamics behind spillover events and the risks to humans. Such efforts could facilitate the development of policy and infrastructure that would help curb the dependency on bushmeat, reduce risks associated with bushmeat harvest, and help understand in what circumstances zoonotic disease spillover events occur.

There is still uncertainty as to how education should be implemented in different regions and what features of such education would be most valuable for local people. Such an effort might consist of surveying rural bushmeat-harvesting populations across Africa and using the resulting data to contextualize priorities and goals in a way that could help standardize education approaches. While some locations in Africa have had extensive research in the scope and impact of bushmeat harvest, much of Africa has been neglected in those efforts. A more developed understanding of the location, scale, and structure of bushmeat harvest throughout the continent would help researchers and policy-makers prioritize efforts related to disease surveillance, education, or aid. The study of zoonotic spillover events related to viruses, while not completely developed, has received far more attention than the related fields of spillover from bacterial or other non-virus pathogens. There is significant interest in pursuing these lines, as they represent an underdeveloped body of knowledge that could have significant impacts related to human health and disease ecology.

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