Chapter 2
Emerging Viral Zoonoses from Wildlife Associated with Animal-Based Food Systems: Risks and Opportunities

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Abstract Zoonotic viruses of wildlife origin have caused the majority of recent emerging infectious diseases (EIDs) that have had significant impacts on human health or economies. Animal consumption-based food systems, ranging from the harvest of free-ranging wild species (hereafter, wild harvest systems) to the in situ stocking of domestic or farmed wild animals (hereafter, animal production systems), have been implicated in the emergence of many of these viruses, including HIV, Ebola, SARS, and highly pathogenic avian influenza (HPAI).

Keywords Animal production systems • Biodiversity • Bushmeat • Climate change • Ebola virus • Ecosystem • Emerging infectious diseases • Food systems • Highly pathogenic avian influenza • Viral zoonosis

Introduction

Zoonotic viruses of wildlife origin have caused the majority of recent emerging infectious diseases (EIDs) that have had significant impacts on human health or economies (Morse et al. 2012; Jones et al. 2008). Animal consumption-based food systems, ranging from the harvest of free-ranging wild species (hereafter, wild harvest systems) to the in situ stocking of domestic or farmed wild animals (hereafter, animal production systems), have been implicated in the emergence of many of these viruses, including

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HIV, Ebola, SARS, and highly pathogenic avian influenza (HPAI) (Karesh et al. 2012b; Zambrana-Torrelio et al. 2012).

At the same time, wild harvest and animal production systems form a fundamental component of food systems more broadly (Milner-Gulland and Bennett 2003; FAOSTAT 2014). Food forms the foundation of human societies, promoting health and wellbeing, and sustaining growing populations (Tilman et al. 2011). The role of wild harvest and animal production systems in the emergence of human and domestic animal diseases thus presents something of a paradox, where ecosystem services meet ecosystem disservices, sometimes with catastrophic consequences.

Here we review the current status of EIDs, and in particular viral zoonoses originating in wildlife, as they relate to wild harvest and animal production systems. We conclude that both systems present considerable proximal and distal risks for disease emergence through a number of mechanisms. The reasons are that they frequently entail or promote human contact with a diversity of wildlife species, unusual assemblages of high numbers and densities of animals, rapid and widespread transportation networks and large-scale environmental perturbation, which are all key risk factors of disease emergence (Daszak et al. 2000; Patz et al. 2004).

More broadly, the costs of wild harvest and animal production systems to global environments are enormous and mounting. The resultant biodiversity loss due to overhunting, and ecosystem loss or degradation due to the expansion of areas suitable for livestock, are major environmental and societal challenges in themselves (Steinfeld et al. 2006; Milner-Gulland and Bennett 2003). In addition to the threat of disease emergence, these impacts contribute to novel and damaging negative feedback costs and a direct toll on other aspects of human health and wellbeing (Raudsepp-Hearne et al. 2010; Schröter et al. 2005; McMichael et al. 2007). To understand the risks, we must look to the combination between direct and indirect risk factors that together shape the disease risks of food systems; for example, the act of consuming a wild animal in addition to the upstream factors, such as deforestation, that can more broadly increase the availability of wildlife for food. To mitigate the risks, we concur with previous authors that opportunities exist to manipulate food systems to provide win-win or more equitable solutions for conservation and health (Tilman et al. 2011; Nelson et al. 2009; McMichael et al. 2007) and to develop or inform preventative policy for better public health and ecosystem health outcomes.

This review will focus on two distinct animal-based food systems that encompass potentially very different risk pathways for disease emergence. First, "animal production systems" are typified by in situ stocking and raising of animals (both domestic and in some cases wild species) at small to very large scales and from low to very high densities. Secondly, "wild harvest systems" typically involve direct harvest of wild, free-roaming animal species (including, for example, "bushmeat"). In some cases these systems, and the disease risks associated with them, are nested or overlap. For example, wild-harvested species can be marketed through outlets that are associated with sophisticated sale and distribution systems (Milner-Gulland and Bennett 2003). Conversely, domesticated or farmed wild species may also be released or allowed to roam shepherded or freely in landscapes, providing opportunities for contact with wild species (Kilpatrick et al. 2009). Nevertheless, we feel that distinguishing between

wild harvest and in situ produced is useful when considering the role of animal-based food systems in the emergence of viral zoonoses.

Scale of Animal Production Systems and Their Importance to Human Health

Since 1950, there have been enormous increases in the production of, and trade in, domestic livestock species used for food (particularly chickens and pigs) (Godfray et al. 2010; FAOSTAT 2014) (Fig. 2.1). Although the density and composition of domestic species varies dramatically globally (Fig. 2.2), livestock systems alone

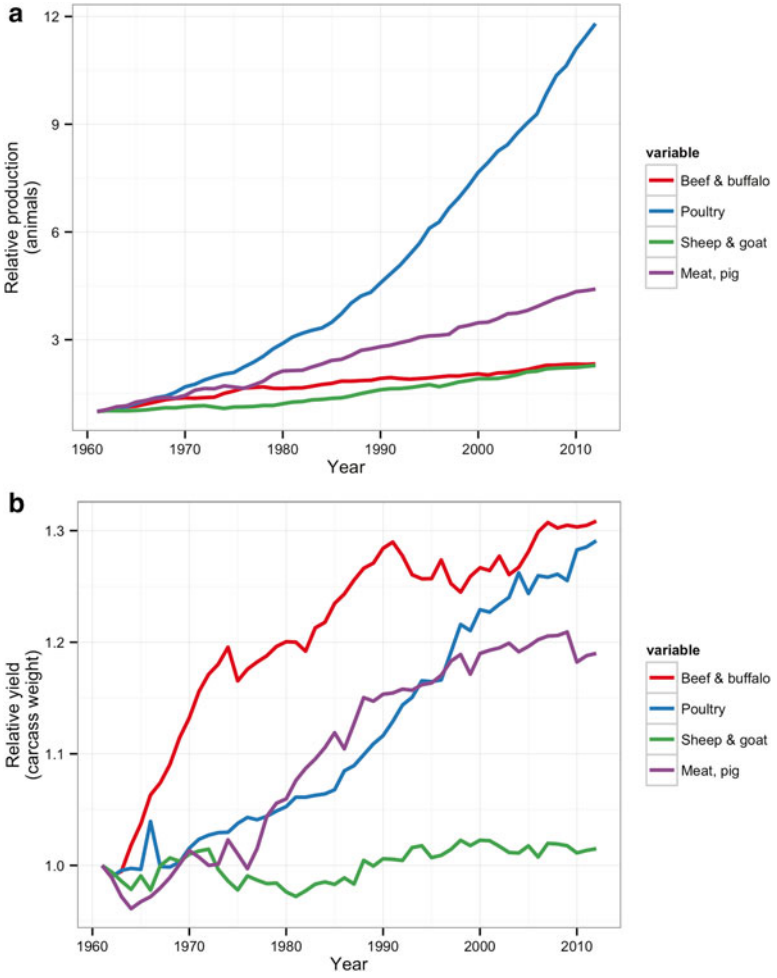

Fig. 2.1 Global trends in livestock production (**a**) and yield (**b**), in relative number of animals and relative carcass weight (hectograms/carcass), respectively, from 1962 to 2014. Livestock production data from Food and Agriculture Organization of the United Nations (FAO), accessible at http://faostat3.fao.org)

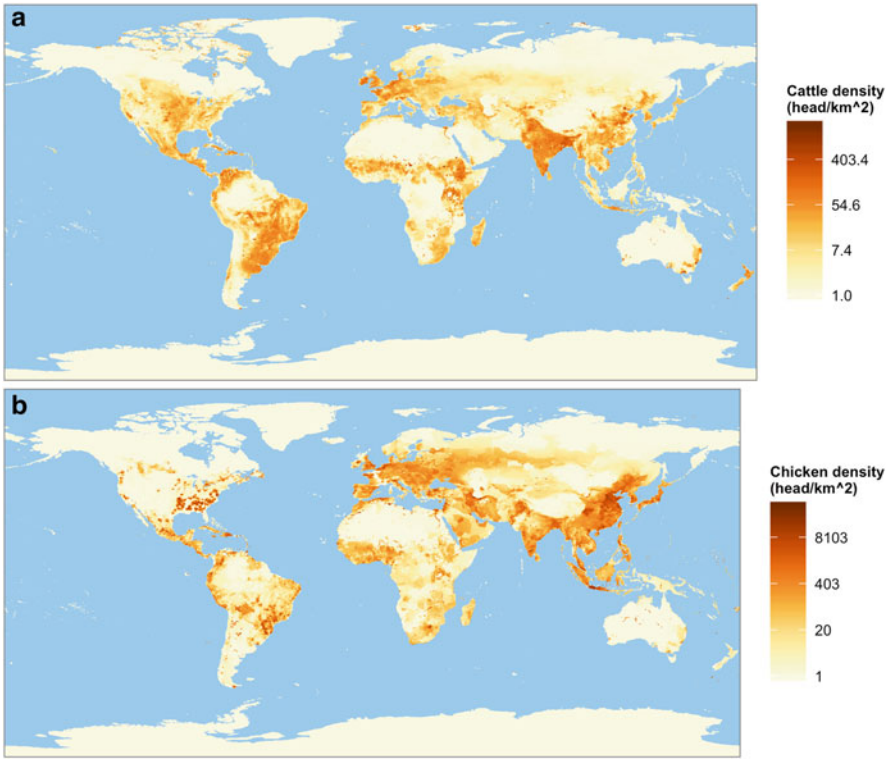

Fig. 2.2 Estimated global distribution of livestock (population density, head/km^2). (**a**) Cattle. (**b**) Chickens. Data from Food and Agriculture Organization of the United Nations (FAO), Gridded Livestock of the World 2.0 (Robinson et al. 2014)

now account for more than 30 % of the Earth's ice-free terrestrial area (Steinfeld et al. 2006). In addition to growing populations, demand for higher volume and higher quality diets has driven these increases, and per capita production has also increased (FAOSTAT 2014). In 2013 there were approximately 3.5 individual poultry and 0.5 common production mammals (cattle, sheep, and pigs) raised, on average, for every one of nearly seven billion people globally (calculated from FAOSTAT 2014). Facilitating this growth, the global capacity to raise both more animals and more animals per unit of land area has increased, marking an increase in efficiency and intensity of food production. The highest densities and efficiencies are achieved with the aid of technological advances that were developed and are primarily used in the developed world (Tilman et al. 2011).

These increases in animal production match or exceed human population growth, which has itself almost tripled over the same period. To put this in context, population growth has been so dramatic over the last century that 7–14 % of all humans ever born remain alive today (Bradshaw and Brook 2014; Westing 2010; PRB 2014). The same statistics for many domestic animals likely exceed this. The sheer scale and

global reach of food production systems means that they are also major drivers of ecosystem change. In addition to the direct risks posed by high stocking densities and sophisticated transportation and trade networks, it is the associated environmental and demographic factors of animal production systems that present some of the biggest challenges from a disease emergence perspective (McMichael et al. 2007).

Scale of Wild Harvest Systems and Their Importance to Human Health

Despite the growth and scale of animal production systems globally, the direct acquisition and consumption of wild meat still forms an important component of local economies and diets, and in many instances holds cultural significance and other preference determinants that enhance its value.

Relative to other sources of meat, the contribution of wild-harvested meat to household diets, nutrition and local livelihoods is highest for the rural poor, who are often underserved by local animal production systems and/or have limited ability to raise animals for a variety of reasons (e.g., environmental constraints, lack of technology) (Brashares et al. 2011). Some populations are essentially dependent on wild-harvested food to meet basic nutritional requirements; for example, in some parts of the Congo Basin, protein from bushmeat comprises as much as 94 % of total protein of the household diet (Fa et al. 2003). In Madagascar, restricting access to bushmeat would reportedly result in a significant increase of anemia cases among children, with the poorest households worst-affected (Golden et al. 2011).

Although people have been hunting wild species for food for millennia, there has been a marked increase in the harvest of wild species over the last several decades (Milner-Gulland and Bennett 2003; Ziegler 2010). For example, the development of industrial logging in Republic of Congo has led to a 69 % increase in the population of logging towns and a 64 % increase in bushmeat supply (Poulsen et al. 2009). The emergence of market-based economies and the commercialization of wild-harvest animals in urban centers have further increased demand. The scale of the trade in wild-harvest meat has also changed considerably due to advances in hunting practices, population growth, and increasing accessibility to remote areas (Nyaki et al. 2014). The trade of wild-harvested meat for food can now be viewed as a continuum ranging from subsistence-based rural consumption to commercial hunting for the international trade in wild animal meat and products (e.g., exotic food and traditional medicine), with this leading to dramatic price point differences (Brashares et al. 2011; Chaber et al. 2010). For example, bushmeat traders have reported pricing per kg of wild meat in Paris markets at up to double the price of domestic meat for sale in French supermarkets (Chaber et al. 2010). Similarly, in New York, USA, smoked duiker (an antelope) from Ghana can be readily attained, although at up to 25 times the cost of the same species sold near its source (Brashares et al. 2011). Such “urban” demand, which also occurs locally, places a premium on

wild species and often permits local hunters to earn incomes comparable to or higher than local wages for other occupations, sustaining commercial hunting on a large scale (Schulte-Herbrüggen et al. 2013). Market factors thus provide a significant additional incentive for wild harvest beyond the protein needs of an individual hunter or family.

The monetary incentives for importation of wild-harvested meat have resulted in extensive trade networks, and an expansion of the public health risk of zoonotic disease spillover. An estimated 5 tons of bushmeat is smuggled through Paris Roissy-Charles de Gaulle airport from Africa per week in passenger baggage (Chaber et al. 2010). Even if the prevalence of potentially zoonotic pathogens in the animals traded is low, and viability of microbes much reduced after time in the trade, the sheer volume of bushmeat traded internationally, and lack of traceability through illegal or clandestine trade, suggests a significant public health risk. Measuring or controlling this risk is made more difficult because the global distribution of wild-harvested food is highly variable, poorly reported, and difficult to map (Fig. 2.3).

Emerging Infectious Diseases Associated with Food Systems

Infectious diseases that appear in a new host (e.g., humans) for the first time or markedly increase in incidence or geographic range, or cause disease with apparently novel clinical patterns are often referred to as emerging infectious diseases (EIDs) (Taylor et al. 2001). Historically, many human diseases are thought to have arisen as a result of the environmental and demographic changes attributable to the advent of food systems (agriculture and/or animal domestication) (Pearce-Duvet 2006; Wolfe et al. 2007). Such "civilization diseases" include some likely acquired directly from domesticated species (e.g., measles, pertussis) or indirectly, either

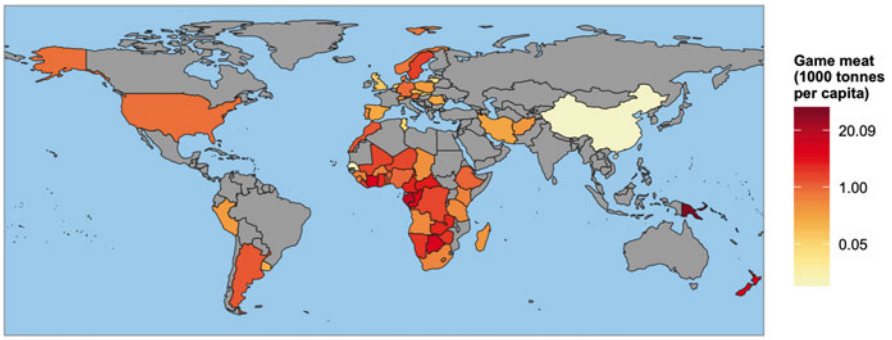

Fig. 2.3 Estimated global production of game meat in tons per capita, yearly average 2000–2009. Livestock production data from Food and Agriculture Organization of the United Nations (FAO), accessible at http://faostat3.fao.org). These data likely reflect a widespread lack of reporting of wild-harvested meat

because domestic animals provided a more stable route of infection for pathogens to enter human populations from wildlife (e.g., smallpox) or due to the influence of environmental perturbation in elevating the risk of pathogen transmission to humans from wildlife hosts and vectors (e.g., *falciparum* malaria) (Pearce-Duvet 2006). All of the diseases mentioned above were at one time EIDs, highlighting how some of the emerging diseases of the recent past and present will almost certainly become the diseases of humanity in the future. Understanding the origins and drivers of EIDs is thus of considerable and growing public health interest (Morse et al. 2012).

Demographic, behavioral, ecological, and climatic changes have all been variably cited as drivers of historical and contemporary disease emergence (Patz et al. 2004, 2008; Smith et al. 2007; Wolfe et al. 2005a, b; Daszak et al. 2000; Morse 1995; Taylor et al. 2001; Foley et al. 2005; Jones et al. 2008). The increasing impact of an exponentially rising human population has led to an increase in these drivers over time which likely explains why the frequency of disease emergence appears to have increased in recent decades, even after correcting for increased capacity and effort to detect them (Pike et al. 2014; Jones et al. 2008). Systems in equilibrium are probably the least likely systems to give rise to EIDs.

The current scale and continued expansion of wild-harvest and animal production systems thus present ongoing opportunities for diseases to emerge into the human population.

Viral Zoonoses of Wildlife Associated with Animal-Based Food Systems

Although rarely observed (approximately 1 per year globally) (Jones et al. 2008), zoonotic viruses that originate in wildlife and are associated with food systems punch above their weight in terms of their potential human, animal, and economic impacts. Some of the best recognized examples include HIV, SARS, Ebola, and Avian Influenza A viruses (Karesh et al. 2012b; Zambrana-Torrelio et al. 2012; Hahn 2000a, b; Heymann 2004a, b), but they also include diseases that have caused significant regional or more local impacts, such as Japanese Encephalitis virus (Mackenzie et al. 2004), a number of rodent-borne hantaviruses (e.g., Junin, Laguna, Machupo viruses) (Epstein 1995; Young et al. 1998a, b; Johnson et al. 1997a, b; Webb et al. 1967a, b), Lassa virus (Ter Meulen et al. 1996), a number of bat-borne viruses (e.g., Nipah, Menanagle viruses) (Calisher et al. 2006; Pulliam et al. 2011; Luby et al. 2006), and monkeypox virus (Parker et al. 2007) (Table 2.1).

Across the spectrum of animal-based food systems described above, there are a range of common features or activities (e.g., capture and handling, butchering, trade, transport, and consumption) that provide opportunities for pathogens to move from wildlife into humans, whether directly or indirectly via a domestic animal link or via vectors. The processes involved, however, can be complex. Below we use the diseases listed in Table 2.1 as examples to decompose these risks into three fundamental com-

Table 2.1 Table detailing food-system-associated disease emergence events, including context, transmission modes, and risk factors identified in literature review

		Circumstances of emergence				Confirmed or probable transmission routes (Jones et al. 2008 categories)					Distal risk factors (documented, probable, unknown)						
Food system	Pathogen or disease	Reservoir species	Location of transmission	Outcome of transmission	Contact event type/ food system risk behavior	Direct contact	Air-borne	Vector-borne	Oral (ingest)	Envir./ fomite	Road building	Deforestation/ agricultural conversion	Climate/ climatic change	Trade	Increasing human connectivity	Agricultural intensification (high population densities/ food storage)	References
Wild harvest	Ebola	Unknown (fruit bats suspected)	DRC, Sudan, Guinea, Sierra Leone	Localized and regional outbreaks	Human–wildlife; hunting and consumption	Yes			Yes	Yes	Greater wildlife access	Increasing niche overlap, stressed food security, greater wildlife access	Shifting species ranges, stressed food security	Local trade in bushmeat	Human to human or international spread		Leroy et al. (2009); Pigott et al. (2014)
	SARS	Horseshoe bats (Rhinolophus spp. infection also found in masked palm civets, pigs)	Guangzhou, Guangdong Province, China	Far-reaching epidemic with person-to-person transmission	Human–wildlife; handling	Yes	Possible, but unlikely				Greater wildlife access	Greater wildlife access		Extensive trade of wild caught species, interspecies mixing in market setting	Human to human or international spread		Li et al. (2005a, b); Wang et al. (2006); Shi and Hu (2008)
	HIV	Chimpanzee, Sooty Mangabey	Africa	Repeated spillover, global pandemic	Human–wildlife; hunting and consumption	Yes					Greater wildlife access	Greater wildlife access			Human to human or international spread		Hahn (2000a, b); Wolfe et al. (2005a, b)
	Lassa virus	Wild rodents (Mastomys natalensis, Natal multi-mammate mouse)	Endemic in Guinea, Liberia, Sierra Leone, and regions of Nigeria	Regional epidemics, with little human-to-human transmission	Human–wildlife; hunting, handling, consumption	Yes	Yes (aero-solized rodent excreta)		Yes (rodent excreta)			Elevated reservoir numbers (greater availability as food)		Local trade in bushmeat		Elevated reservoir numbers around grain storage	Heymann (2004a, b)

Animal production	Influenza A virus	Aquatic birds, poultry, swine. Infection found in other mammals.	Widespread. Azerbaijan, Cambodia, China, Djibouti, Egypt, Indonesia, Iraq, Lao People's Democratic Republic, Myanmar, Nigeria, Pakistan, Thailand, Turkey, Vietnam.	Localized outbreaks	Wildlife–domestic animal–human; farming activities	Yes	Yes		Yes			Land clearance for domestic production	Shifting species ranges (poultry–wildlife contact), stressed food security (increased poultry numbers and densities)	Increased global food demand	Increased pandemic risk	Agricultural intensi-fication	Heymann (2004a, b)
	Japanese encephalitis virus	Pigs (mostly asymptomatic amplifying host), wading birds (reservoir host), mosquito vector	East, South-East, South Asia	Epidemics, but without human-to-human transmission (humans are dead-end hosts)	Vector-domestic animal, vector-human; farming activities			Yes (mos-quito)				Land clearance and flooding for rice and pig production (increased vector population, domestic animal amplifier)	Shifting species ranges (mosquito), stressed food security (increased pig numbers and densities)	Increased food demand		Agricultural intensi-fication	Campbell et al. (2011); Centers for Disease Control (2013)

(continued)

Table 2.1 (continued)

		Circumstances of emergence				Confirmed or probable transmission routes (Jones et al. 2008 categories)					Distal risk factors (documented, probable, unknown)						
Food system	Pathogen or disease	Reservoir species	Location of transmission	Outcome of transmission	Contact event type/ food system risk behavior	Direct contact	Air-borne	Vector-borne	Oral (ingest)	Envir./ fomite	Road building	Deforestation/ agricultural conversion	Climate/ climatic change	Trade	Increasing human connectivity	Agricultural intensification (high population densities/ food storage)	References
	Nipah virus	Fruit bats (Pteropus spp.)	Malaysia, Bangladesh	Localized outbreaks	Wildlife–domestic animal–human; farming activities (also consumption of contaminated date palm sap in Bangladesh)	Yes			Yes			Increasing niche overlap (bat hosts losing habitat)	Shifting species ranges (bat hosts), stressed food security (increased pig numbers and densities, mixed cropping)	Increased food demand		Agricultural intensi-fication	Luby et al. (2006); Rahman et al. (2010); Pulliam et al. (2011)
	Menangle virus	Fruit bats (suspected reservoir host), pigs (amplifier host)	Australia (Menangle)	Localized spill-over	Wildlife–domestic animal–human; farming activities	Yes						Increasing niche overlap (bat hosts losing habitat)	Shifting species ranges (bat contact with pigs)	Increased food demand		Agricultural intensi-fication	Kirkland et al. (2001); Center for Food Security and Public Health (2007)
Agricultural	Junin virus (Argentine hemorrhagic fever)	Rodents (Calomys musculinus, dry lands vesper mouse; Calomys laucha, small vesper mouse)	Buenos Aires	Localized outbreaks (endemic in region)	Wildlife excreta–human; agricultural activities	Yes	Yes (aerosolized rodent excreta)		Yes (rodent excreta)			Elevated reservoir numbers				Elevated reservoir numbers around food storage	Maiztegui (1975); Public Health Agency of Canada (2010)

	Laguna Negra virus (Hantavirus pulmonary syndrome)	Calomys laucha (vesper mouse)	Bolivia, Paraguay, Chile	Localized outbreaks	Wildlife excreta–human; agricultural activities		Yes (aerosolized rodent excreta)					Elevated reservoir numbers				Elevated reservoir numbers around food storage	Johnson et al. (1997a, b); Young et al. (1998a, b)
	Machupo virus (Bolivian hemorrhagic fever)	Calomys callosus (vesper mouse)	Bolivia	Localized outbreaks	Wildlife excreta–human; agricultural activities		Yes (aerosolized rodent excreta)					Elevated reservoir numbers				Elevated reservoir numbers around food storage	Webb et al. (1967a, b)
	Monkeypox virus	Unknown, multiple (rodents, including Gambian rats, striped mice, dormice, rope and tree squirrels; primates)	Democratic Republic of Congo, Sudan, elsewhere in Congo Basin and western Africa. Cases also seen in Midwestern United States	Localized outbreaks	Wildlife–human; handling, contact with infected animals and people or bodily fluids thereof	Yes						Elevated reservoir numbers		Extensive trade of wild caught species	Human to human or international spread		World Health Organization (2011)
	Lassa virus	Wild rodents (Mastomys natalensis, Natal multimammate mouse)	Endemic in Guinea, Liberia, Sierra Leone, and regions of Nigeria	Regional epidemics, with little human-to-human transmission	Wildlife excreta–human; agricultural activities	Yes	Yes (aerosolized rodent excreta)		Yes (rodent excreta)			Elevated reservoir numbers				Elevated reservoir numbers around food storage	Heymann (2004a, b)

Color shadings relate to importance to the event, based on our judgment from our literature review. Darker factors are more proximate or directly related to the event

ponents—the types of contact events associated with them, the various transmission pathways that are involved, and the upstream distal risk factors that promote the former to facilitate emergence. These together help highlight the activities and conditions common to food systems that may promote disease emergence.

Contact

Contact events provide the "proximal" risk interfaces that allow disease transmission. Contact events can occur in many different contexts but their common feature is that they provide the opportunity for the transmission of a pathogen. Transmission interfaces could include: human–wildlife, human–vector, human–domestic animal, human–human, wildlife–vector, wildlife–domestic animal, and vector–domestic animal contact. The diversity of types of contact that have been relevant historically for the emergence of viral zoonoses from wildlife associated with food systems is summarized in Table 2.1. In wild harvest systems, contact events have typically occurred directly between a person and a range of wildlife species ultimately used for food (HIV, Ebola, SARS, Lassa, Monkeypox), via contact activities such as hunting, handling, butchering, consumption, and trade. In animal production systems, people have become infected most commonly from contact with domestic animals that had first been exposed to wildlife pathogens (e.g., HPAI influenza, Nipah, Menangle), where tending and treating domestic animals for illness resulted in human infection. Japanese Encephalitis represents an example where humans are infected when bitten by mosquito vectors, which acquire and maintain infection after feeding on wild hosts or infected domestic species (e.g., pigs). For diseases more diffusely associated with agricultural activities, infection often occurs via contact with virus present in wildlife excreta (e.g., hantaviruses) or fomites (see Table 2.1 and references therein).

Transmission Routes

While contact events serve as the fundamental infection interface, different types of contact may carry very different levels of "riskiness" depending largely on the mode of transmission of a given pathogen. An important challenge in understanding the risks of viral zoonoses due to food systems is identifying the relevant transmission routes that allow for pathogen transmission between wild animal reservoirs, vectors, domestic animals, and humans. Transmission routes can be classified into five broad but distinct categories and used to analyze patterns of disease emergence (Loh et al. 2015). These include direct contact (i.e., skin-to-skin contact; scratches; animal bites; contact with body fluids, organs, and tissues; direct large droplet >5 μm exposure), airborne (i.e., via dust particles and airborne small droplets <5 μm), vector-borne (i.e., by biting or mechanical transfer by arthropods), oral (i.e., consumption

of contaminated food or water; ingestion of arthropods), and contamination (i.e., indirect contact with soil or vegetation, contact with water, indirect transmission by contaminated inanimate objects). Direct contact is the most common transmission pathway cited for diseases associated with food systems, although airborne transmission of virus associated with aerosolized wildlife excreta is also relatively common (Table 2.1). Nevertheless, the range of transmission pathways implicated in the emergence of viral zoonoses from food systems is relatively diverse, with each transmission pathway represented at least once.

Distal Factors

While the type of contact, mediated by the various transmission pathways, represents the proximal risk factor for spillover (i.e., where and how transmission takes place), other factors may promote or reduce the likelihood that contact events occur in the first place or result in pathogen transmission, thereby altering the risk of emergence. These distal or upstream risk factors also include any condition or activity along any transmission pathway that intensifies the contact rate, increases the prevalence or diversity of available pathogens to be transmitted, or elevates the likelihood of successful disease transmission given contact (Murray and Daszak 2013; Lloyd-Smith et al. 2009). Distal risk factors could also include other "enabling" factors, such as climate or other environmental factors. The key distal factors that have been associated with the emergence of viral zoonoses from food systems are summarized in Table 2.1. Broadly speaking, large-scale ecosystem and environmental change, including deforestation, land-use change and conversion for agriculture, have been commonly implicated in disease emergence within food systems. Examples include the rodent-borne arenaviruses (Lassa, Junin, Machupo, Laguna Negra) that are often facilitated by agricultural land conversion, HIV which is thought to have emerged as a result of the changes in forest access and human connectivity attributable to industrial development, and Nipah and Menangle viruses which are thought to have emerged due to increasing niche overlap and contact between reservoirs and domestic animal species (see Table 2.1 and references therein). In addition to human-induced ecosystem changes, there are a range of social and demographic factors that have also played roles as distal risk factors, including the trade of wildlife species within markets with sophisticated transport networks and in which inter-species mixing has occurred (SARS, monkeypox), or increased domestic animal stocking densities (agricultural intensification) to meet growing human food demands while at the same time enhancing conditions for viral amplification (HPAI, Japanese Encephalitis) (see Table 2.1 and references therein).

If the diversity of previous disease emergence mechanisms is anything to go by, forecasting disease risks within food systems should not rely solely on historical precedence. While decomposing the risks of disease emergence into subcategories of proximal and distal risk factors can seem trivial, particularly for the well-known examples examined here (Table 2.1), the real utility and application of this approach

is for forecasting future risks (see Sect. 4.3 below). Such horizon scanning exercises are critical for anticipating the risks associated with the growth in scale and magnitude of food systems into the future. For example, in industrial food systems, airborne transmission may potentially be an under-recognized pathway as a recent study found a million-fold elevated concentration of aerosolized invisible dust in a poultry barn fan compared to the outside air (Leibler et al. 2009). This could have implications for both human and animal health in addition to the spread of true airborne diseases such as Foot and Mouth disease (FMD), influenza, or Q fever.

Future Trends in Food Acquisition and Production Systems: Implications for Viral Zoonoses

Both the acquisition of food from wild sources as well as the scale and intensity of animal production systems are projected to continue increasing over the coming decades (McMichael et al. 2007; The World Bank June 2012; Zambrana-Torrelio et al. 2012). This presents challenges for disease emergence and for environmental stability as increasing global populations demand higher dietary quantity and quality leading to continued land-use change and deforestation, expansion of global trade and travel networks and potential secondary impacts through climate change, biodiversity loss, and other outcomes.

Wild Harvest Trends

Harvesting wild animals for food and other uses has been increasing in the recent past, and is likely to continue its growth as one of the greatest threats to biodiversity (Fa et al. 2002). This follows increasing reliance on wild animals to meet dietary needs for protein under conditions of food insecurity in many regions, especially developing countries in the tropics (Fa et al. 2003). Exploitation of wildlife for food will likely be facilitated by increasing land-use change and deforestation activities, whatever their purpose, particularly in more remote regions where these activities make forests more accessible to hunters and create new markets for bushmeat (Poulsen et al. 2009). Climate change is also expected to threaten food security in many regions, again promoting greater reliance on wild harvest species in some regions (Nkem et al. 2010). This is set against a background of exponentially increasing global air travel which already poses a significant risk to global health via the transportation of pathogens (Hufnagel et al. 2004), and is likely to promote increased global trade in wild-harvested meat.

The development of roads may represent one of the most significant ways of increasing opportunities for wild harvest. Roads are considered critical infrastructure developments that can improve access to technologies, healthcare and educa-

tion, forming a key component of many countries' development plans. Approximately 60 % more roads are projected by 2050 compared to 2010, mostly in developing countries (Dulac 2013), potentially making road building one of the most significant drivers of future environmental change (Laurance et al. 2014). Road building has already increased the risk of some diseases associated with human development (e.g., agricultural intensification), with an increase in number of cases of human hantavirus reported following the completion of a highway through the Brazilian Amazon (Medeiros et al. 2010). Road building, particularly on such a large scale, will almost certainly further facilitate bushmeat hunting in the most biodiverse regions of the planet and change the scale at which people are able to move wild animals out of newly exploited areas and into commodity chains, thereby increasing public health risks.

Animal Production Trends

Global food production is forecast to approximately double by 2050 to meet the food demands of a global population that is expected to plateau at around nine billion people (Godfray et al. 2010; Tilman et al. 2011). The biggest growth will be seen in domestic animal products, with predictions suggesting an increase in annual demand for meat of 6–23 kg per person per year worldwide by 2050. The largest increases will be in Latin America, the Caribbean, South East Asia and the Pacific, and demand per person will more than double in sub-Saharan Africa (Thornton and Herrero 2010). Food production is expected to more intensely compete with the acquisition of other products from the environment such as land, water and energy, contributing to loss of ecosystem services and biodiversity, including some related to health (Tilman et al. 2011; McMichael et al. 2007). Deforestation and associated human activities related to domestic animal production, for example, will continue to alter the structure and species composition of ecosystems and increase contact rates between humans, wildlife, vectors and domestic animals, resulting in disease emergence (Murray and Daszak 2013).

Food production will also continue to contribute to, and be strongly affected by, climate change (Godfray et al. 2010; McMichael et al. 2007), particularly in developing and less developed countries, and this will coincide with changes in disease risk. For example, climate change may influence some key elements of the avian influenza A transmission cycle. Climate change is expected to influence migration patterns of migratory bird species that are the natural reservoirs for many AI viruses, alter transmission dynamics and affect the survival of virus outside of hosts, all of which have the potential to shift disease risks for this important group of viruses (Gilbert et al. 2008). In addition, the link between domestic duck production, which is expected to grow in scale and extent to build food security in Asia, and the persistence of HPAI H5N1 is often synchronously linked to the production of rice. The strong seasonal component of this system means that climate change has the poten-

tial to impact the distribution and persistence of HPAI in other more indirect ways as well (Gilbert et al. 2008).

The increasing intensification of food production, marked by high animal densities and stressful conditions, may facilitate rapid spread of diseases among immunocompromised and genetically similar animals, potentially compromising food security and posing zoonotic disease risks. In addition to the risk of wildlife origin zoonoses making their way into humans via a domestic animal intermediary, the widespread use of antimicrobials in food production, primarily for non-therapeutic growth promotion in livestock and aquaculture production, may introduce rapid selection pressure for resistant bacterial and viral strains and further contribute to disease risks. While drug-resistant EIDs are more common in non-zoonotic EIDs than zoonotic EIDs (Zambrana-Torrelio et al. 2012), greater use of growth-promoting antimicrobials in animal production and human exposure via food as well as antimicrobials disseminated into the environment from animal production waste may potentially increase human susceptibility to infections (Marshall and Levy 2011).

Additionally, as intensification occurs, biosecurity measures become all the more necessary. For example, a lag in biosecurity practices during increases in poultry production has been attributed to the evolution of HPAI H5N1 in poultry flocks, which caused extensive impacts to the poultry and public health sectors, leading to mortality or culling of over 200 million birds, as well as several hundred human deaths (Karesh et al. 2012a). The lack of adequate infrastructure for biosecurity measures in low-income nations where bushmeat currently serves as a major form of subsistence nutrition thus presents vulnerability around potential intensified livestock production to shift protein sources. Agricultural practices may also pose risks to wildlife, including flow of pathogens between livestock and wild species, in addition to the more usual culprits of habitat destruction or degradation.

Looking Forward: Intervention and Risk Mitigation Options

The range of both proximal and distal risk factors associated with disease emergence from food systems makes effective disease management a complex and daunting proposition. However, this also provides opportunities for mitigation and adaptation with a view to better managing food systems to reduce environmental and biodiversity impacts in addition to disease risks in the future. For proximal risk factors associated with specific contact events, better safety and biosecurity standards will be a core part of any strategy to reduce disease risks from wild harvest and animal production systems. However, the more distal drivers of disease emergence (e.g., land-use change) or global changes that occur in step with, or that directly facilitate, the expansion of food systems present a much more nebulous and diffuse range of risks. Managing these underlying drivers may ultimately provide solutions for sustainability and public health threats. We propose that direct

mitigation of disease transmission is thus only ever going to be a part of what urgently needs to be a much more encompassing, proactive strategy targeting the distal risks of disease emergence (Murray et al. 2012). This requires a novel response that could be rooted in holistic cost–benefit analyses of total ecosystem services (Costanza et al. 2014).

Win-Win Solutions for Conservation and Health?

The number of hungry people globally has declined by more than 200 million since 1990, despite the addition of almost two billion people over the same period (FAO 2014). This largely can be attributed to ongoing improvements and increases in global food production and supply systems and global efforts to improve food security (FAO 2014). These improvements have improved human health more broadly by decreasing malnourishment, increasing life expectancy and reducing child mortality (Raudsepp-Hearne et al. 2010; Godfray et al. 2010). Health gains will of course continue to be an ongoing human objective, with food security being a central part of the development agenda (FAO 2014). The health benefits of food production, however, need to be weighed against the health and environmental costs, including those associated with ecosystem degradation (McMichael et al. 2007). There have been calls for concerted redistribution of excess food and deployment of food production technologies to areas of the world most in need (Tilman et al. 2011). These strategies might have secondary benefits to global health by reducing food demands in some regions, leading to reduced environmental and total area designated for food production.

Health and conservation goals and actions have not always aligned, with history of some rash disease control efforts unnecessarily resulting in harm to wildlife and domestic animal populations, and when conservation frameworks (e.g., the Convention on International Trade in Endangered Species of Wild Fauna and Flora) do not directly consider disease risks in their decision making. To more effectively address both public health and conservation concerns, it is necessary to improve synergy between the two communities with integrated, science-based approaches. This need is especially urgent in the food safety realm, where nutritional dependencies demand sustainable access to food sources. The UN's post-2015 Sustainable Development Goals set the stage for poverty reduction, food access/security, health, and environmental balance, potentially providing opportunities for integrated solutions that could be applied to food safety challenges related to wildlife and food systems.

The underlying drivers of disease emergence from wildlife are also the same main pressures that drive biodiversity loss as identified by the UN Convention on Biological Diversity Global Biodiversity Outlook 4, namely habitat loss, degradation and fragmentation, overexploitation of wildlife, unsustainable production in agriculture and other industries, and impact of invasive species (Secretariat of the Convention on Biological Diversity 2014). In addition, emerging viruses are not

only threats to humans, but may also be pathogenic to susceptible wild host species. There is thus a compelling opportunity for co-benefits for conservation and public health through collaborative efforts.

The Policy Landscape

Despite the globalization of food supply systems, there is no central global governance structure for foodborne or food-associated disease risks, and there is no precise estimate of foodborne or food-associated disease incidence or burden. To address this, the World Health Organization (WHO) is undergoing an assessment of the global impacts of foodborne illnesses through its Department of Food Safety and Zoonoses. While the FAO-WHO Codex Alimentarius provides benchmark international trade standards to promote food safety, the guidance is voluntary; the U.S., for example, does not require its producers and suppliers to adhere to its rigorous standards. The lack of a central authority for wildlife health has translated into limited infrastructure for disease surveillance and control around the safety of bushmeat in both source and demand settings. As a result, efforts have largely focused on reactive responses to disease emergence events, rather than prevention of disease risks. The World Organization for Animal Health (OIE) regulates trade of livestock for priority diseases, which include some potential zoonoses (e.g., HPAI), but does not address wildlife trade/pathogens specifically in its World Trade Organization-enforced sanitary standards. There is no comparable regulation for wildlife diseases, although in the USA, the U.S. Centers for Disease Control and Prevention specifically restricts imports of certain turtles in response to salmonellosis, bats in response to Nipah virus, African rodents in response to monkeypox, civets in response to SARS, and non-human primates (Smith et al. 2012).

Risk Analysis

Greater knowledge of disease emergence risks from wildlife can inform identification of key areas for intervention. Risk assessment is commonly conducted in food safety to identify vulnerabilities in the food supply, but more fully protecting health requires determining and addressing upstream or distal risks of viral emergence from harvested wild meat. Employing risk analysis tools can assist in science-based policies by anticipating and identifying ways to mitigate risk, as well as identifying priority knowledge gaps for research investments to refine future analyses. The structure of a formal risk analysis can help provide continuity and objectivity in the process, involving problem description, hazard identification, risk assessment, risk management, implementation and review, and risk communication throughout. More proactive risk analysis efforts can systematically identify critical control points for conservation and health benefits, and congruence among both where synergies can be maximized.

For example, the OIE-IUCN Guidelines for Wildlife Disease Risk Analysis promote analysis of disease risk in an ecosystem, rather than single-species, context (World Organisation for Animal Health (OIE) & International Union for Conservation of Nature (IUCN) 2014). This perspective can help determine conservation risks as well as zoonotic disease risks. While uncertainty and complexity inherently exist in wildlife disease risk analysis (Jakob-Hoff et al. 2014), useful information can be gained, especially for viral disease threats where initial knowledge on transmission pathways and pathogen dynamics can enable best practices to reduce risks while more information is gathered.

Realistic Interventions

Harvesting of wild meat holds a critical position in the diets, economies, and cultures of millions of people globally. Current governance and enforcement structures are therefore unlikely to be fully effective and in many cases unwarranted for reducing local demand (e.g., for local populations living in or on the periphery of forests with few suitable alternatives). In this context, some interventions may be low-resource and high-yield, such as working with hunters and foresters to convey risks of collecting deceased wildlife carcasses and encourage reporting of animal morbidity or mortality that can inform disease surveillance efforts (Rouquet et al. 2005; Olson et al. 2012). These interventions to prevent initial spillover are especially important given the challenges of influencing human behaviors when controlling human outbreaks. For example, the UN recently reported the dismissal of a local chief in Sierra Leone for failing to report secret burials that may have violated regulations intended to contain the spread of Ebola (UN Mission for Ebola Emergency Response (UNMEER) 19 November 2014). However, it seems inevitable that reducing demand for bushmeat will be fundamentally necessary to safeguard species from overhunting and extinction and to mitigate the disease risks. Reducing demand will be easiest for populations with access to alternative food sources. High demand and pricing for wild-harvest species may influence hunting practices, including expanding volumes and time of year spent hunting, whereas previously hunting pressure has been naturally limited by hunting for subsistence, traditional techniques, seasonality, and cultural taboos on harvesting certain species (Lindsey et al. 2012).

Strong regulations can be established to prohibit and provide disincentives for legal and illegal sale of bushmeat to overcome growing demand as a luxury product. High taxation levies may sufficiently raise the price to reduce demand and provide revenue for enforcement and surveillance efforts (see Courchamp et al. 2006). The clandestine nature of the illegal wildlife trade remains a challenge for tracking and enforcement, but high penalties have not yet been enacted in many settings; steeper penalties may provide stronger disincentives to participation in the illegal wildlife trade, such that even if zero volume cannot be realistically achieved, a large reduction in volume will still have large benefits from a risk reduction viewpoint. Additionally,

development projects that encroach into wildlife habitat can be managed to ensure they do not fuel demand for bushmeat. Governments can demand responsibility on the part of corporations to provide alternative food sources for employees and set policies to provide deterrents for bushmeat consumption. Governments could require wildlife disease risk analysis processes to be undertaken for proposed development projects to more proactively weigh risks and ensure risk prevention or mitigation measures are conducted. This type of analysis could be included within existing Health Impact Assessment (HIA) structures, because, while some HIAs include risk of zoonotic diseases from domestic animals and other vectors, few adequately address the range of potential zoonotic pathogens in their intended scope.

Can the Farming of Wildlife Become a Safe Alternative to Wild-Harvest Meat?

The farming of wildlife for food may reduce pressures on wild populations, and is increasingly becoming a way to sustain demand in the face of increasing prices of wild-caught individuals. For example, porcupines, snakes, frogs, tigers, and a range of other wildlife species are farmed in Southern China for food and medicine (Abbott and van Kooten 2011). While this has been debated widely as a tool for conservation (e.g., the farming of tigers to reduce poaching), it has not been proposed as a strategy to reduce the public health risks of the wildlife trade. We propose that the farming of wildlife species could reduce the risk of zoonotic disease spillover if similar health and biosecurity measures are applied to farmed wildlife as to livestock. In this scenario, specific known zoonoses are tested for, treated or infected animals removed from a farm's founder wild-caught stock, resulting in reduced risk of zoonotic pathogen "spillover" to ranchers, traders, or butchers. Biosecurity measures will be critical to reducing risk because the intensive production of species that potentially carry novel zoonotic agents could result in increased pandemic risk. For example, civets have long been farmed in some parts of Africa (Eniang and Daniel 2007; Tolosa and Regassa 2007), and prior to the SARS outbreak in China in 2002, civets were farmed increasingly in China. While the role of civets in the emergence of SARS is not fully understood, it is thought that they may have acted as amplifier hosts, expanding transmission and evolution of a bat-origin SARS-like coronavirus (Wang and Eaton 2007).

Wildlife ranching (typically lower density, semi-free ranging stock) may provide a more suitable production option in areas where more conventional and higher intensity animal production is not supported. For example, regions with tsetse fly infestations affect cattle production through high morbidity and mortality burden from trypanosomiasis; while wildlife appear to carry infection, they are not highly susceptible to it (Steverding 2008). In theory, wildlife ranching may provide a contained environment where disease may be controlled through adoption of effective biosecurity measures. For example, Zambia's wildlife ranching is subject

to inspection of animals or meat by veterinarians prior to sale (Lindsey et al. 2013). However, the sensitivity of this approach in detecting disease risks is not known; visual inspections by veterinarians may not recognize all illness in animals, especially asymptomatic infections that wildlife may be carrying, and viral pathogens are often not evident in meat without laboratory screening. Challenges around traceability in the market chain also introduce risk if free-ranging and ranched animals cannot be distinguished.

Ranch-raised wild animals may also potentially come into greater contact with wildlife (e.g., if ranches are at the periphery of protected areas), potentially shifting the dynamics of population genetics and pathogen flow. Since the main risk pathways from viral zoonoses originating in wildlife associated with animal production systems come from the spillover of wildlife pathogens to domestically farmed species, more research is needed on disease risks in wildlife farms versus in free-ranging wildlife, as well as the development of formal guidelines on biosecurity and other practices to reduce risks to and from native wildlife, such as guidelines on proximity to conserved areas.

Conclusions, Gaps, and Future Research Needs

Several key research gaps remain that limit our ability to recognize and prioritize needs for viral threat reduction related to wildlife. Firstly, we lack knowledge of most of the viral pathogens that are circulating in wildlife (most of which have not yet been discovered and characterized (Anthony et al. 2013)), and how those pathogens are evolving in relation to our changing pressures on the environment. Secondly, we lack criteria to fully determine zoonotic potential of viral agents that are detected. Progress in these research areas is important for identifying practices that drive disease transmission risks and for prioritizing critical control points in risk analyses and risk reduction efforts (Morse et al. 2012).

Current surveillance systems for viral zoonoses are highly reactive, largely capturing threats once they have emerged in humans or have caused extensive livestock or wildlife morbidity or mortality. While current systems are inadequate for prevention and early detection, existing programs may be leveraged as a starting point (Murray et al. 2012). For example, many countries conduct wild bird surveillance for avian influenza, but screening is typically limited to only a subset of HA and NA subtypes, limiting knowledge of viral diversity circulating in populations (Hoye et al. 2010). Targeted surveillance for broader indicators of viral diversity (e.g., whole genome sequencing or at least typing for all 8 AI gene segments) can provide baseline monitoring to capture changes, including risk potential, over time. Coordinated global research priorities, such as set forward by the OIE-FAO OFFLU global network of expertise on influenza (http://www.offlu.net/), can provide an international platform for systematic surveillance approaches and data aggregation and identify high-priority investment areas to maximize surveillance resources.

To sufficiently respond to viral disease threats that are identified by surveillance, a coordinated, multi-disciplinary system is needed. The currently siloed mandates

of intergovernmental organizations and government departments limit the actionable utility of data. To move forward at a global level, investments made toward achievement of OIE Performance of Veterinary Service (PVS) and the WHO's International Health Regulations might expand capabilities related to pathogen surveillance in wildlife.

Partners from the biodiversity community also have a strong role for participation, through conservation efforts that are increasingly recognizing the risks of infectious disease agents to wildlife populations (e.g., great ape die-offs from infection with Ebola). The UN's Convention on Biological Diversity recently "recognized the value of a One Health approach" toward shared health and biodiversity benefits at its 12th Conference of the Parties in October 2014, and also has addressed sustainable use of biodiversity in terms of bushmeat and sustainable wildlife management, providing a possible entry for work on both topics by CBD member countries.

Additionally, critical areas of need for collaboration can be identified under the CBD-WHO Joint Work Programme on Biodiversity and Human Health. On a national level, including through integration into CBD members' National Biodiversity Strategies and Action Plans, laboratories can be modified or constructed to serve human and animal health screening needs, avoiding potential duplication of resources, and enabling closer collaboration among human and animal health authorities and researchers (Murray et al. 2012). A phase change in the broadening of health toward an ecosystem perspective is needed to truly maximize cross-disciplinary synergies.

The USAID Emerging Pandemic Threats PREDICT program has developed viral pathogen discovery programs in wildlife at high-spillover risk interfaces in 20 developing countries that are "hotspots" for disease emergence (http://www.vetmed.ucdavis.edu/ohi/predict/). The protocols could be implemented more widely, including in national surveillance systems. Surveillance can be targeted to assess risks at food-associated interfaces, such as wildlife hunting, markets where bushmeat is present, and restaurants serving wildlife.

In addition to the benefits for strengthening public health capacity and infrastructure, there is a strong overall cost argument to detecting and preventing viral disease emergence from bushmeat and other wildlife sources. A recent study using ground-truthed data for viral discovery in bat species estimated that around 300,000 viruses exist in mammalian wildlife, 85 % of which could be detected through investments of approximately US$1.4 billion. Aiming for 100 % detection would be more expensive ($6.8 billion) due to diminishing returns on viral discovery, but even this figure is less than the cost of some major single outbreaks (e.g., SARS) (Anthony et al. 2013), and far less than the total costs of emerging zoonotic diseases over the past two decades, estimated to be in the order of hundreds of billions of dollars (The World Bank June 2012; Karesh et al. 2012a). Globally coordinated, mitigative responses that reduce the risks and frequency of diseases emerging in the first place and are implemented now are forecast to save approximately US$3.5 billion per year over a 100-year time horizon in comparison to a business-as-usual approach to EID response (Pike et al. 2014).

References

Abbott B, van Kooten GC (2011) Can domestication of wildlife lead to conservation? The economics of tiger farming in China. Ecol Econ 70(4):721–728. doi:10.1016/j.ecolecon.2010.11.006

Anthony SJ, Epstein JH, Murray KA et al (2013) A strategy to estimate unknown viral diversity in mammals. mBio 4(5):e00513–e00598

Bradshaw CJA, Brook BW (2014) Human population reduction is not a quick fix for environmental problems. Proc Natl Acad Sci 111(46):16610–16615. doi:10.1073/pnas.1410465111

Brashares JS, Golden CD, Weinbaum KZ et al (2011) Economic and geographic drivers of wildlife consumption in rural Africa. Proc Natl Acad Sci 108(34):13931–13936

Calisher CH, Childs JE, Field HE et al (2006) Bats: important reservoir hosts of emerging viruses. Clin Microbiol Rev 19(3):531–545

Campbell GL, Hills SL, Fischer M, Jacobson JA, Hoke CH, Hombach JM et al (2011) Estimated global incidence of Japanese encephalitis: a systematic review. Bull World Health Organ 89(766–774):774A–774E

Center for Food Security & Public Health (2007) Menangle virus infection. University, IS

Centers for Disease Control (2013). Japanese Encephalitis. http://www.cdc.gov/japaneseencephalitis/. Accessed 25 Nov 2014

Chaber AL, Allebone Webb S et al (2010) The scale of illegal meat importation from Africa to Europe via Paris. Conserv Lett 3(5):317–321

Costanza R, de Groot R, Sutton P et al (2014) Changes in the global value of ecosystem services. Glob Environ Chang 26:152–158. doi:10.1016/j.gloenvcha.2014.04.002

Courchamp F, Angulo E, Rivalan P et al (2006) Rarity value and species extinction: the anthropogenic allee effect. PLoS Biol 4(12), e415. doi:10.1371/journal.pbio.0040415

Daszak P, Cunningham A, Hyatt A (2000) Emerging infectious diseases of wildlife – threats to biodiversity and human health. Science 287:443–449

Dulac J (2013) Global land transport infrastructure requirements: Estimating road and railway infrastructure capacity and costs to 2050. International Energy Agency, Paris

Eniang EA, Daniel W (2007) Revisiting the age-long African civet farming in Ethiopia against the backdrop of increasing animal welfare concerns: what strategies for sustainable utilization and conservation? Walia 25:34–40

Epstein PR (1995) Emerging diseases and ecosystem instability: new threats to public health. Am J Public Health 85(2):168–172

Fa JE, Peres CA, Meeuwig J (2002) Bushmeat exploitation in tropical forests: an intercontinental comparison. Conserv Biol 16(1):232–237

Fa JE, Currie D, Meeuwig J (2003) Bushmeat and food security in the Congo Basin: linkages between wildlife and people's future. Environ Conserv 30(01):71–78

FAO (2014) State of food insecurity in the world: in brief. Food and Agriculture Organization of the United Nations, Rome

FAOSTAT (2014) Food and agriculture organization of the United Nations Statistics Division. http://faostat3.fao.org/browse/FB/*/E

Foley JA, DeFries R, Asner GP et al (2005) Global consequences of land use. Science 309(5734):570–574

Gilbert M, Slingenbergh J, Xiao X (2008) Climate change and avian influenza. Rev Sci Tech 27(2):459

Godfray HCJ, Beddington JR, Crute IR et al (2010) Food security: the challenge of feeding 9 billion people. Science 327(5967):812–818

Golden CD, Fernald LC, Brashares JS et al (2011) Benefits of wildlife consumption to child nutrition in a biodiversity hotspot. Proc Natl Acad Sci 108(49):19653–19656

Hahn BH (2000a) AIDS as a zoonosis: scientific and public health implications. Science 287(5453):607–614. doi:10.1126/science.287.5453.607

Hahn BH (2000b) AIDS as a zoonosis: scientific and public health implications. Science 287:607–614

Heymann DL (2004) Control of communicable diseases manual. American Public Health Association Publications, Washington, DC
Hoye BJ, Munster VJ, Nishiura H et al (2010) Surveillance of wild birds for avian influenza virus. Emerg Infect Dis 16(12):1827–1834. doi:10.3201/eid1612.100589
Hufnagel L, Brockmann D, Geisel T (2004) Forecast and control of epidemics in a globalized world. Proc Natl Acad Sci U S A 101(42):15124–15129
Jakob-Hoff RM, MacDiarmid SC, Lees C et al (2014) Manual of procedures for wildlife disease risk analysis. World Organisation for Animal Health in association with the International Union for Conservation of Nature and the Species Survival Commission, Paris
Johnson M, Bowen MD, Ksiazek TG et al (1997a) Laguna Negra virus associated with HPS in western Paraguay and Bolivia. Virology 238(1):115–127. doi:10.1006/viro.1997.8840
Johnson M, Bowen MD, Ksiazek TG, Williams RJ, Bryan RT, Mills JN et al (1997b) Laguna Negra virus associated with HPS in western Paraguay and Bolivia. Virology 238:115–127
Jones KE, Patel NG, Levy MA et al (2008) Global trends in emerging infectious diseases. Nature 451:990–994
Karesh WB, Dobson A, Lloyd-Smith JO et al (2012a) Ecology of zoonoses: natural and unnatural histories. Lancet 380(9857):1936–1945. doi:10.1016/S0140-6736(12)61678-X
Karesh WB, Loh E, Machalaba C (2012b) Food safety: a view from the wild side. In: Choffnes ER, Relman DA, Olsen L, Hutton R, Mack A (eds) Improving food safety through a one health approach: workshop summary. National Academies Press, Washington, DC, http://www.ncbi.nlm.nih.gov/books/NBK114500/
Kilpatrick AM, Gillin CM, Daszak P (2009) Wildlife–livestock conflict: the risk of pathogen transmission from bison to cattle outside Yellowstone National Park. J Appl Ecol 46(2):476–485. doi:10.1111/j.1365-2664.2008.01602.x
Kirkland PD, Love RJ, Philbey AW, Ross AD, Davis RJ, Hart KG (2001) Epidemiology and control of Menangle virus in pigs. Aust Vet J 79:199–206
Laurance WF, Clements GR, Sloan S et al (2014) A global strategy for road building. Nature 513:229–232
Leibler JH, Otte J, Roland-Holst D et al (2009) Industrial food animal production and global health risks: exploring the ecosystems and economics of avian influenza. Ecohealth 6(1):58–70
Leroy EM, Epelboin A, Mondonge V, Pourrut X, Gonzalez J-P, Muyembe-Tamfum J-J et al (2009) Human Ebola outbreak resulting from direct exposure to fruit bats in Luebo, Democratic Republic of Congo, 2007. Vector Borne Zoonotic Dis 9:723–728
Li W, Shi Z, Yu M, Ren W, Smith C, Epstein JH et al (2005a) Bats are natural reservoirs of SARS-like coronaviruses. Science 310:676–679
Li Y, Huang X, Yu ITS, Wong TW, Qian H (2005b) Role of air distribution in SARS transmission during the largest nosocomial outbreak in Hong Kong. Indoor Air 15:83–95
Lindsey P, Balme G, Becker M et al (2012) Illegal hunting and the bush-meat trade in savanna Africa: drivers, impacts and solutions to address the problem. Panthera/Zoological Society of London/Wildlife Conservation Society report, New York, p 74
Lindsey PA, Barnes J, Nyirenda V et al (2013) The Zambian wildlife ranching industry: scale, associated benefits, and limitations affecting its development. PLoS One 8(12), e81761. doi:10.1371/journal.pone.0081761
Lloyd-Smith JO, George D, Pepin KM et al (2009) Epidemic dynamics at the human–animal interface. Science 326(5958):1362–1367. doi:10.1126/science.1177345
Loh E, Olival KJ, Zambrana-Torellio C et al (2015) Targeting transmission pathways for emerging zoonotic disease surveillance and control. Vector Borne Zoonotic Dis 15(7):432–437
Luby SP, Rahman M, Hossain MJ et al (2006) Foodborne transmission of Nipah virus, Bangladesh. Emerg Infect Dis 12:1888–1894. doi:10.3201/eid1212.060732
Mackenzie JS, Gubler DJ, Petersen LR (2004) Emerging flaviviruses: the spread and resurgence of Japanese encephalitis, West Nile and dengue viruses. Nat Med 10:98–109
Maiztegui JI (1975) Clinical and epidemiological patterns of Argentine haemorrhagic fever. Bull World Health Organ 52:567–575
Marshall BM, Levy SB (2011) Food animals and antimicrobials: impacts on human health. Clin Microbiol Rev 24(4):718–733. doi:10.1128/CMR.00002-11

McMichael AJ, Powles JW, Butler CD et al (2007) Food, livestock production, energy, climate change, and health. Lancet 370(9594):1253–1263
Medeiros D, Rosa ES, Marques AA et al (2010) Circulation of hantaviruses in the influence area of the Cuiabá-Santarém Highway. Mem Inst Oswaldo Cruz 105(5):665–671
Milner-Gulland E, Bennett EL (2003) Wild meat: the bigger picture. Trends Ecol Evol 18(7):351–357
Morse SS (1995) Factors in the emergence of infectious-diseases. Emerg Infect Dis 1(1):7–15
Morse SS, Mazet JA, Woolhouse M et al (2012) Prediction and prevention of the next pandemic zoonosis. Lancet 380(9857):1956–1965
Murray KA, Daszak P (2013) Human ecology in pathogenic landscapes: two hypotheses on how land use change drives viral emergence. Curr Opin Virol 3(1):79–83. doi:10.1016/j.coviro.2013.01.006
Murray KA, Skerratt LF, Speare R et al (2012) Cooling off health security hot spots: getting on top of it down under. Environ Int 48:56–64. doi:10.1016/j.envint.2012.06.015
Nelson E, Mendoza G, Regetz J et al (2009) Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Front Ecol Environ 7(1):4–11
Nkem J, Kalame FB, Idinoba M et al (2010) Shaping forest safety nets with markets: adaptation to climate change under changing roles of tropical forests in Congo Basin. Environ Sci Policy 13(6):498–508
Nyaki A, Gray SA, Lepczyk CA et al (2014) Local scale dynamics and local drivers of bushmeat trade. Conserv Biol 28(5):1403–1414
Olson SH, Reed P, Cameron KN et al (2012) Dead or alive: animal sampling during Ebola hemorrhagic fever outbreaks in humans. Emerg Health Threats J 5. doi:10.3402/ehtj.v5i0.9134
Parker S, Nuara A, Buller RML et al (2007) Human monkeypox: an emerging zoonotic disease. Future Microbiol 2:17–34
Patz JA, Daszak P, Tabor GM et al (2004) Unhealthy landscapes: policy recommendations on land use change and infectious disease emergence. Environ Health Perspect 112(10):1092–1098
Patz JA, Olson SH, Uejio CK et al (2008) Disease emergence from global climate and land use change. Med Clin North Am 92(6):1473–1491. doi:10.1016/j.mcna.2008.07.007
Pearce-Duvet JM (2006) The origin of human pathogens: evaluating the role of agriculture and domestic animals in the evolution of human disease. Biol Rev 81(3):369–382
Pigott DM, Golding N, Mylne A, Huang Z, Henry AJ, Weiss DJ et al (2014) Mapping the zoonotic niche of Ebola virus disease in Africa. eLife 3
Pike J, Bogich T, Elwood S et al (2014) Economic optimization of a global strategy to address the pandemic threat. Proc Natl Acad Sci U S A 111(52):18519–18523. doi:10.1073/pnas.1412661112
Poulsen JR, Clark CJ, Mavah G et al (2009) Bushmeat supply and consumption in a tropical logging concession in Northern Congo. Conserv Biol 23(6):1597–1608. doi:10.1111/j.1523-1739.2009.01251.x
PRB (2014) How many people have ever lived on earth? Population Reference Bureau. http://www.worldometers.info/world-population/#total
Public Health Agency of Canada (2010) Junin Virus. http://www.phac-aspc.gc.ca/lab-bio/res/psds-ftss/junin-eng.php. Accessed 25 Nov 2014
Pulliam JRC, Epstein JH, Dushoff J et al (2011) Agricultural intensification, priming for persistence and the emergence of Nipah virus: a lethal bat-borne zoonosis. J R Soc Interface 9(66):89–101
Rahman SA, Hassan SS, Olival KJ, Mohamed M, Chang LY, Hassan L et al (2010) Characterization of Nipah virus from naturally infected Pteropus vampyrus bats, Malaysia. Emerg Infect Dis 16:1990–1993
Raudsepp-Hearne C, Peterson GD, Tengö M et al (2010) Untangling the environmentalist's paradox: why is human well-being increasing as ecosystem services degrade? BioScience 60(8):576–589. doi:10.1525/bio.2010.60.8.4
Robinson TP, Wint GRW, Conchedda G et al (2014) Mapping the global distribution of livestock. PLoS One 9:e96084–e96084

Rouquet P, Froment JM, Bermejo M et al (2005) Wild animal mortality monitoring and human Ebola outbreaks, Gabon and Republic of Congo, 2001–2003. Emerg Infect Dis 11(2):283–290. doi:10.3201/eid1102.040533
Schröter D, Cramer W, Leemans R et al (2005) Ecosystem service supply and vulnerability to global change in Europe. Science 310(5752):1333–1337. doi:10.1126/science.1115233
Schulte-Herbrüggen B, Cowlishaw G, Homewood K et al (2013) The importance of bushmeat in the livelihoods of West African cash-crop farmers living in a faunally-depleted landscape. PLoS One 8(8), e72807
Secretariat of the Convention on Biological Diversity (2014) Global biodiversity outlook 4. Secretariat of the Convention on Biological Diversity, Montreal, QC
Shi Z, Hu Z (2008) A review of studies on animal reservoirs of the SARS coronavirus. Virus Res 133:74–87
Smith KF, Sax DF, Gaines SD et al (2007) Globalization of human infectious disease. Ecology 88(8):1903–1910
Smith KM, Anthony SJ, Switzer WM et al (2012) Zoonotic viruses associated with illegally imported wildlife products. PLoS One 7(1), e29505. doi:10.1371/journal.pone.0029505
Steinfeld H, Gerber P, Wassenaar T et al (2006) Livestock's long shadow: environmental issues and options. Food and Agriculture Organization of the United Nations, Rome
Steverding D (2008) The history of African trypanosomiasis. Parasite Vectors 1(1):3. doi:10.1186/1756-3305-1-3
Taylor LH, Latham SM, Woolhouse MEJ (2001) Risk factors for human disease emergence. Philos Trans R Soc Lond Ser B Biol Sci 356(1411):983–989
Ter Meulen J, Lukashevich I, Sidibe K et al (1996) Hunting of peridomestic rodents and consumption of their meat as possible risk factors for rodent-to-human transmission of Lassa virus in the Republic of Guinea. Am J Trop Med Hyg 55(6):661–666
The World Bank (2012) People, pathogens, and our planet: economics of one health. Report No. 69145-GLB. The World Bank, Washington, DC
Thornton PK, Herrero M (2010) The Inter-linkages between rapid growth in livestock production, climate change, and the impacts on water resources, land use, and deforestation. Policy Research Working Paper 5178. The World Bank
Tilman D, Balzer C, Hill J et al (2011) Global food demand and the sustainable intensification of agriculture. Proc Natl Acad Sci 108(50):20260–20264
Tolosa T, Regassa F (2007) The husbandry, welfare and health of captive African civets (Vivera civetica) in western Ethiopia. Anim Welfare 16(1):15–19
UN Mission for Ebola Emergency Response (UNMEER) (2014) External situation report, 19 Nov 2014
Wang LF, Eaton BT (2007) Bats, civets and the emergence of SARS. Curr Top Microbiol Immunol 315:325–344
Wang LF, Shi Z, Zhang S, Field H, Daszak P, Eaton BT (2006) Review of bats and SARS, pp 1834–1840
Webb PA, Johnson KM, Mackenzie RB, Kuns ML (1967) Some characteristics of machupo virus, causative agent of bolivian hemorrhagic fever. Am J Trop Med Hyg 16(4):531
Westing AH (2010) All the many humans ever: an update. BioScience 60(10):777
Wolfe ND, Daszak P, Kilpatrick AM (2005) Bushmeat hunting, deforestation, and prediction of zoonotic disease emergence. Emerg Infect Dis 11(12):1822–1827
Wolfe ND, Dunavan CP, Diamond J (2007) Origins of major human infectious diseases. Nature 447(7142):279–283
World Health Organization (2011) Monkeypox. http://www.who.int/mediacentre/factsheets/fs161/en/. Accessed 25 Nov 2014
World Organisation for Animal Health (OIE) & International Union for Conservation of Nature (IUCN) (2014) Guidelines for Wildlife Disease Risk Analysis. OIE, in association with the IUCN and the Species Survival Commission, Paris
Young JC, Mills JN, Enria DA et al (1998a) New world hantaviruses. Br Med Bull 54(3):659–673. doi:10.1093/oxfordjournals.bmb.a011718

Young JC, Mills JN, Enria D, Dolan NE, Khan S, Ksiazek TG (1998b) New world hantaviruses. Br Med Bull 54:659–673

Zambrana-Torrelio C, Murray KA et al (2012) One Health and hotspots of food-borne EIDs. In: Choffnes ER, Relman DA, Olsen L, Hutton R, Mack A (eds) Improving food safety through a one health approach: workshop summary. National Academies Press, Washington, DC, http://www.ncbi.nlm.nih.gov/books/NBK114500/

Ziegler S (2010) Application of food balance sheets to assess the scale of the bushmeat trade in Central Africa. Traffic bulletin, vol 22. TRAFFIC International, Cambridge