Disease and Human/Animal Interactions

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Keywords
zonoses, anthroponoses, primates, EcoHealth, One Health, conservation medicine, anthrozoology, biophilia, emerging infectious diseases, bushmeat, companion animals, ecotourism, ethnoprimatology

Abstract
Understanding pathogen exchange among human, wildlife, and livestock populations, and the varying ecological and cultural contexts in which this exchange takes place, is a major challenge. The present review contextualizes the risk factors that result from human interactions with livestock, companion animals, animal exhibits, wildlife through nature-based tourism, and wildlife through consumption. Given their phylogenetic relatedness to humans, primates are emphasized in this discussion; primates serve as reservoirs for several human pathogens, and some human pathogens can decimate wild primate populations. Anthropologists must play a central role in understanding cultural variation in attitudes toward other species as well as perceived risks when interacting with animals. I argue that the remediation of emerging infectious diseases will be accomplished primarily through human behavioral changes rather than through efforts in pathogen discovery. Given the history of human interactions with wildlife, candid discussions on zoonotic diseases will be increasingly important for our combined survival.
INTRODUCTION

The human species has depended on other animals for almost the entirety of its existence; a knowledge of natural systems and animal behavior has been essential to its survival. Even the earliest depictions of art are dedicated to the representation of animals (Valladas et al. 2001). Animals have been central to human life for food, protection, clothing, shelter, medicine, adornment, ritual, and entertainment. Today, interaction with live (particularly wild) animals is much more limited (for many populations) than it used to be. Yet human captivation with the natural world (Fromm 1964), including suggested innate tendencies to emotionally affiliate with other living organisms (“biophilia”; Wilson 1984, Kellert & Wilson 1993), remains strong in most of us. For some it means deep emotional attachment to, and even reverence and ethical responsibility for, many different elements (from landscapes to particular species), and for others it means the dominionistic desire to control the natural world (Kellert 1996). The interdisciplinary field of human–animal studies (“anthrozoology”) aims to contextualize human interactions with non-humans and to understand the range of emotional responses we have toward these species. It is particularly important to contextualize our interactions with nonhuman primate species, as we are members of the Primate order. The subject of “ethnoprimateology” aims to assess and contextualize the roles that humans and other primates have in each other’s lives and to understand how ecological, social, and biological spaces are shared at the human–other primate interface (Fuentes 2012). The present review functions to investigate the consequences of human–animal interactions for infectious disease transmission, with particular emphasis on primates. Understanding the connections between humans and animals and the environments in which we cohabit is the purview of “One Health.” This conceptualization, that the health of humans, other species, and entire ecosystems is interdependent, is not a new one, beginning with Billings (1884) and becoming popularized by Schwabe (1984). The general framework is based on the concept of consilience, or the convergence of evidence (Whewell 1840), in this case the collaborative efforts of physicians, public health professionals, veterinarians, social scientists, and others. This transdisciplinary science, sometimes referred to as “ecosystem health” or EcoHealth (Wilcox et al. 2012), implies an inclusive study of the broad determinants and indicators of health across species and biomes, which is relevant particularly in the current Anthropocene epoch in which humans are modifying the global environment in complex and accelerated ways. The application of this approach to the explicit management/maintenance of protected species and habitats, particularly in the face of global environmental change, and with an understanding of the role of biodiversity in maintaining ecosystem health, has been referred to as “conservation medicine” (Aguirre et al. 2002). Whatever term people choose to use, connections among all species are clearly complex, and understanding the health outcomes of these connections will continue to be hindered by a traditional, compartmentalized approach to health-related research and practices (Kahn et al. 2012). Understanding infectious disease exchange at the interface of human, wildlife, and livestock populations, and the varying ecological and cultural contexts in which this exchange takes place, represents a major challenge and requires committed collaborations that also transcend international borders.

DISEASE EMERGENCE

Pathogens are infectious organisms (viruses, prions, bacteria, protozoa, nematodes, cestodes, trematodes, and fungi) that parasitize other organisms, and this state of metabolic dependence results in host illness/impairment (disease). There are at least 1,415 infectious organisms that cause pathogenic disease in humans (Taylor et al. 2001). A majority of these are helminths (32%), bacteria (31%), or viruses/prions (19%), and most are transmitted by indirect (61%, respiratory or
EIDs: emerging infectious diseases

Emerging infectious diseases (EIDs) are defined here as infectious organisms that exhibit increased incidence (number of new cases in a given period of time) in a host population as the result of a number of different factors. They could be newly identified in humans or other vertebrate (livestock or wildlife) hosts. They could be newly evolved and discovered or more likely the result of cross-species transmission (spillover) into new hosts (recipients) from a reservoir species (donors; the biotic source where a pathogen normally lives). They could have moved into new geographic areas, be reemerging (i.e., those that used to cause familiar disease, showed improvement over time, and are now increasing in incidence again, sometimes owing to antimicrobial resistance and decreasing frequency of some immunizations), or even be intentionally released (e.g., biological weapons). They can represent local epidemics or global, pandemic emergence. More than 300 EIDs have been described since 1940 (Jones et al. 2008), although many organisms classified now as EIDs may have long affected us but are now being identified because of new diagnostic methods and increased surveillance (Gire et al. 2012).

Seventy-five percent of EIDs are considered of animal origin (Taylor et al. 2001). Some of the deadliest infectious diseases in human history have originated from wildlife, including the Black Death (\textit{Yersinia pestis}) and the 1918 Spanish influenza. Other well-known examples include rabies from bats (Wood et al. 2012, Luís et al. 2013), as well as many pathogens transmitted from domesticated animals, such as brucellosis (\textit{Brucella melitensis}) via unpasteurized milk (Corbel 2006) and the Middle East respiratory syndrome coronavirus (MERS-CoV) from dromedary camels (\textit{Camelus dromedarius}) (Muller et al. 2015). Livestock and other domesticated animals can serve as bridges for pathogen exchange between humans and wildlife. Furthermore, the transmission of human pathogens to animals (known as anthropozoonoses; sometimes referred to as anthrozoontanies, zoonanthroponoses, or reverse zoonoses) has and continues to be a significant problem (Messener et al. 2014), particularly for wildlife conservation.

The study of EIDs gained popularity in the early twentieth century (Lederberg et al. 1992), yet investigators are only now closer to understanding the dynamics of disease emergence and the factors that play central roles in the transmission of EIDs relevant to human health. Microbial diversity (“zoonotic pool”; Daszak et al. 2001), primarily within livestock and wildlife, serves as the primary source of pathogens available in an area. Although the diversity of vertebrate reservoir hosts in an area provides an origin for infectious organisms, biodiversity remains critical for minimizing pathogen transmission to human hosts (Keeling et al. 2010, Harris & Dunn 2013). This “zooprophylaxis” has been specifically demonstrated for West Nile virus (Swaddle & Calos 2008) and Lyme disease (LoGiudice et al. 2008).

“Spillover” (Daszak et al. 2000) of a pathogen from one species to another usually requires repeated reintroductions before the pathogen becomes established in the new host species; most cross-species transmission events represent “chatter” (Wolfe et al. 2005a) with no sustained transmission throughout otherwise dead-end hosts. These “host shifts” (Antonovics et al. 2002) then usually involve some changes in both the pathogen and the host to establish effective transmission between members of the new host species (Flanagan et al. 2012). That is, a pathogen can become...
endemic within a new species and area only once there is effective human-to-human transmission (Wolfe et al. 2007). The persistence of pathogens in a host population then depends on the presence of susceptible hosts (which otherwise might become resistant, leave the area, or die) (Anderson & May 1991). All of these factors vary by mode of transmission, pathogen virulence (and other organismal characteristics such as length of latency and infectivity), and amount of human intervention, among others.

Microbial adaptations that result from frequent mutations (e.g., antigenic drift in influenza viruses) and host–parasite coevolution (e.g., reassortment and antigenic shift in influenza viruses) contribute to host switching. Many of these are RNA viruses that readily undergo recombination (Worobey & Holmes 1999) (note that this is not necessarily the case for negative-stranded RNA viruses; Holmes 2003). The pathogens must find ways around host defenses (e.g., tetherin, a protein that inhibits infection from some retroviruses in humans; Neil et al. 2008), so these organisms are selected to evolve high viral loads in infected hosts and to require low infection doses (Bailey et al. 2015). Many of these pathogens have high environmental persistence so that they can live outside of hosts for extended periods of time, and many of these have broad host ranges (i.e., infecting multiple mammalian orders) (Cleaveland et al. 2001, Woolhouse et al. 2001). Pathogens with reservoir hosts that span across large geographic ranges and have “fast” life-history traits (e.g., high reproductive rates, large litters, early age at first birth, etc.), such as rodents (Han et al. 2015), are likely candidates for the promotion of disease emergence.

The likelihood of infection greatly depends on host susceptibility factors, including reduced genetic diversity through inbreeding (Keller & Waller 2002, Acevedo-Whitehouse et al. 2003), and immune status varies by the presence of coinfections, general condition (e.g., access to proper nutrition), age, and sex. Phylogenetic relatedness among host species may facilitate more cross-species transmission events because of similar immune responses and cellular receptors (Woolhouse et al. 2012), which appears to be the case for humans and other primates that share susceptibility to many pathogens (Davies & Pedersen 2008). Because humans and other primates share susceptibility, many safety precautions are taken to minimize occupational exposure with captive primates (Muchmore 1976, Inst. Lab. Anim. Res. 2003, Murphy et al. 2006, Bailey & Mansfield 2010, Wolfensohn & Lloyd 2013).

“Pathogen pollution” (Cunningham et al. 2003) of new habitats and host species results from various anthropogenic factors that directly alter exposure to parasitic organisms (Morens et al. 2004, Weiss & McMichael 2004). Changes in land use and land cover include deforestation to accommodate human population growth, natural resource demands, and agricultural expansion (Millenn. Ecosyst. Assess. 2005). Fragmentation produces a “fence effect” (Dobson & May 1986) or “edge effect” (Patz et al. 2004) with a mixture of habitats and land uses, which alters the ecology of pathogens, predators, prey, and all other biota in these patches. The particular effects of habitat fragmentation on parasites in wild primates remain equivocal (Young et al. 2013).

Other ecological changes that modify the likelihood of disease emergence include alterations of surface water (which can provide sources of contamination with parasites and bacteria, as well as changes in breeding sites for mosquitoes, flies, snails, and other vectors) and agricultural development (with correlated contamination by livestock and the overuse of fertilizers and antibiotics). The presence of livestock allows for secondary amplification of some viruses (e.g., Rift Valley fever, *Phlebovirus*) and the mixing of different pathogens from wildlife (e.g., swine and avian influenzas reassorting). Livestock located in communities that border the habitats of wild and endangered species can act as a reservoir for intestinal parasites that can then be transmitted between people and wild animals (Nizeyi et al. 2002, Bekker et al. 2012, Hogan et al. 2014). Agricultural land also provides an area where wildlife may overlap with human communities through “crop-raiding” (the consumption and destruction of agricultural products) (Osborn & Hill 2005). Wild primates
are particularly problematic in this regard because they often visit trash cans/dumpsters, latrines, and shared, contaminated water supplies (Wenz-Mücke et al. 2013).

Climate change, predominantly alterations in temperature and rainfall patterns, can alter host ranges and have multiple effects on the competence, activity, and distribution of arthropod vectors, as well as reservoirs such as rodents. For example, the risk of malaria transmission is higher in cultivated areas that have elevated surface-water temperatures with higher mosquito (*Anopheles* spp.) abundance (Pascual et al. 2006) and a shortened parasite development time (Afrane et al. 2006). Global warming is associated with the spread of a suitable habitat for the deer tick (*Ixodes scapularis*), the primary vector for Lyme disease (Brownstein et al. 2005). The El Niño Southern Oscillation (ENSO) effect has been associated with outbreaks of Hantavirus pulmonary syndrome (caused by the Hantaan virus, family Bunyaviridae) in the US Southwest owing to changes in deer mice (*Peromyscus maniculatus*) populations (Engelthaler et al. 1999), and Dengue virus has become more prevalent in temperate areas owing to the expanded geographic range of the *Aedes aegypti* mosquito (Hales et al. 2002). The Nipah virus (family Paramyxoviridae) outbreak in Southeast Asia (in 1999) was linked with drought produced by ENSO, deforestation for the expansion of oil palm plantations, and the resultant displacement of bats (flying fox, genus *Pteropus*) that began feeding on orchards near pig farms (Chua et al. 2002).

Human behaviors that alter the likelihood of exposure to new reservoir hosts are clearly associated with pathogen emergence. These include human movement (urbanization, sprawl, suburbanization, travel, and migration/refugee resettlement; Kimball et al. 2005), changes in population densities with correlated changes in sanitation, trade of goods (particularly animals), and even denial about the risks of infection and other sociocultural changes. But clearly, the primary theme in this growing body of literature on EIDs in humans is the central role of the changes in patterns of human contact (particularly the rate and intensity of physical proximity) with wildlife and domestic animals. The contexts in which our species interacts with animals vary significantly; the following discussion focuses on animals as entertainment and food and the associated pathogen transmission potential.

**ANIMALS AS ENTERTAINMENT**

“We can understand, too, that natural species are chosen not because they are good to eat but because they are good to think.”

—Lévi-Strauss (1964, p. 89)

Today we interact with animals in various ways and many of them for the explicit purpose of entertainment. These include private animal collections (originally to demonstrate wealth), traveling entertainment venues such as circuses (where animals are forced to perform unnatural behaviors), rodeos, dog and horse racing, and animal fighting. Two hundred and thirty-three zoos and aquariums are currently accredited by the Association of Zoos and Aquariums in the United States (AZA 2016), and 183 million people visited these facilities in 2014 (J. Wright, personal communication). Zoos provide important education programs, and they participate in captive breeding and cooperative species-management programs. They stimulate visitor interest in nature (Falk et al. 2007, Clatton et al. 2009), and research suggests that people express positive emotional bonds with animals, show greater concern for both wild and domestic species, and are more willing to support conservation programs as a direct result of their visits (Ascione & Weber 1996, Kellert 1996, Allen et al. 2002). Others contend that zoos and similar facilities provide basic animal-directed entertainment
with few measurable effects on animal and habitat conservation (Morgan & Hodgkinson 1999, Balmford et al. 2008, Marino et al. 2010).

What is unequivocal is that zoos do bring together a variety of exotic species into a mixture of habitats. Regardless of biosecurity measures, gastrointestinal parasites are particularly common in these captive animals (Roy et al. 2009, Berrilli et al. 2011, David et al. 2014, Li et al. 2015). Animal caretakers are sometimes infected with these pathogens, which can be particularly dangerous for primate caretakers exposed to cercopithecine herpesvirus 1 (Herpesvirus B; Inst. Lab. Anim. Res. 2003, Murphy et al. 2006), an alphaherpesvirus endemic in Asian macaques that can result in fatal meningoencephalitis in humans in the absence of antiviral treatment (Holmes et al. 1995). Given the amount of contact we, as a species, had and continue to have with macaques, the number of people infected with cercopithecine herpesvirus 1 is low, with 50 reported cases since 1932 (CDC 2016) and with all fatalities recorded from biomedical research settings (Huff & Barry 2003).

Visits to agricultural fairs, open farms, farmers’ markets, petting zoos, and other temporary animal exhibits present additional opportunities of zoonotic disease transmission, especially for pathogens such as *Escherichia coli* O157:H7, *Salmonella enterica*, and *Cryptosporidium parvum* (Crump et al. 2002, LeJeune & Davis 2004, Porten et al. 2006). Opportunities for children to feed captive animals have been associated with several epidemics (Heuvelink et al. 2002, Bender & Shulman 2004). This practice can be very problematic for immunocompromised individuals, which is one reason why hand washing is usually encouraged after such activities (Stirling et al. 2008).

Human contact with wildlife in association with nature-based tourism presents additional opportunities for pathogen transmission. Ecotourism increasingly brings people into contact with potential reservoirs of infection and with endangered species that are highly susceptible to our human pathogens. This kind of activity can be particularly problematic for primates (Muehlenbein & Ancrenaz 2009) (Figure 1); many of these species are immunologically naïve to human pathogens, and primate populations can be decimated quickly because of their slow reproductive rates. Tourists’ relative contribution to the spread of pathogens to wildlife is largely unknown, but the number of people visiting wildlife sanctuaries worldwide is going to increase. Those visiting wildlife sanctuaries underestimate the contribution they may have to other animals, as well as the risk of becoming infected themselves (Muehlenbein & Ancrenaz 2009). For example, ecotourists concerned about environmental protection, with recognized travel itineraries to view endangered species, are not adequately protected against many vaccine-preventable diseases (Muehlenbein et al. 2008). They are largely unaware of their true vaccination status, and they underestimate the risks they pose to other species. Furthermore, these same travelers to wildlife sanctuaries are oftentimes ill, showing specific signs and symptoms of infection (particularly those associated with respiratory diseases that can easily be transmitted to wildlife) (Muehlenbein et al. 2010).

Despite their attractiveness, primates can be very aggressive toward tourists, particularly when the animals are being fed (Brennan et al. 1985) (Figure 2). Biting is common in chacma baboons (*Papio ursinus*) at the Cape Peninsula, South Africa (Hoffman & O’Riain 2011), Barbary macaques (*Macaca sylvanus*) in Gibraltar (Fa 1992), and long-tailed macaques (*M. fascicularis*) in Bali, Indonesia (Fuentes & Gamerl 2005). Because of these bites, a significant proportion of travelers to Southeast Asia (Bali in particular) receive rabies postexposure treatment after returning home (Kardamanidis et al. 2013) [even though there have been only ~25 cases of human rabies caused by primates (Favoretto et al. 2001, Gautret et al. 2014)]. Using reports submitted to the GeoSentinel global surveillance network, which monitors travel-related illness and injury (a consortium of approximately 60 travel medicine clinics and hundreds of affiliate members across the globe), Gautret et al. (2007) report only 320 cases of animal-associated injuries (bites and scratches) between 1998
and 2005. A more recent and detailed analysis reveals a minimum of 1,051 cases of monkey bites in travelers reported between 1995 and April 2016 (M. Mendelson & M. Muehlenbein, unpublished data). Many of these exposures occur at holy places where, because of their sacred status in Hinduism, Buddhism, and the Shinto faith, monkeys are often tolerated. And many of these animals are known to carry organisms that are infectious to and possibly pathogenic in humans.
Figure 2
Primates, particularly macaques, can be aggressive toward tourists. Shown are (a) Barbary macaque (*Macaca sylvanus*) in the Upper Rock area of the Gibraltar Nature Reserve, and (b) long-tailed macaque (*M. fascicularis*) at the Wat Khao Lad temple in Hua Hin, Thailand. Photographs by A. Klegarth.

For example, a high proportion of rhesus macaques (*M. mulatta*) at temples in Kathmandu, Nepal, are infected with various retroviruses, including simian foamy viruses (SFVs), cercopithecine herpesvirus 1, and simian virus 40 (Jones-Engel et al. 2006). Similar results have been found in Bali, Indonesia, with long-tailed macaques (*M. fascicularis*) infected with cercopithecine herpesvirus 1 (Engel et al. 2002) and SFVs (Engel et al. 2006).

Human contact with companion animals represents another avenue by which pathogens may be exchanged between groups. The global trade in domesticated and wild animals as personal companions is staggering, with more than 1.68 billion animals traded in the United States between the years 2000 and 2006 (Smith et al. 2009). Exotic pet ownership (i.e., nondomesticated animals) has a long history by our species; even the Harrods department store in London sold large carnivores as companion animals for many decades. However, private ownership of these animals is very risky (Nyhus et al. 2003); oftentimes people consider such animals as docile beasts, an inaccurate assumption that often leads to fatal outcomes (Tuan 1984), and most caretakers lack the necessary information to properly support exotic animals in captivity. Disease transmission is an often overlooked cause of morbidity and mortality from privately owned animals, yet pet-associated infections in humans are common (Morris et al. 2012, Stull et al. 2015). These include *Pasteurella multocida* (pasteurellosis) from large carnivores, *Francisella tularensis* (tularemia) from rabbits, *Chlamydophila psittaci* (psittacosis) from birds, *Capnocytophaga canimorsus* from dogs, *Toxoplasma gondii* (toxoplasmosis) from cats, and even *Aeromonas hydrophila* from alligators (Weber & Rutala 1999). *Salmonella* infection in humans from pet reptiles and amphibians occurs frequently (Woodward et al. 1997, Burnham et al. 1998), as do intestinal parasite infections from dogs (Awadallah & Salem 2015). Monkeypox (*Orthopoxvirus*) even made its way into the United States because of the pet trade: Rodents shipped from Ghana to Texas in 2003 were held in a quarantine facility with North American prairie dogs that acquired the virus and were sold as pets, resulting in almost 50 human cases of infection (Hutson et al. 2007).
Figure 3

(a) Pig-tailed macaques (Macaca nemestrina) being sold as pets at the Pramuka Bird Market in Jakarta, Indonesia. Photograph by A. Klegarth. (b) Young primates (and small-sized species) are used as pets throughout the world, even in the United States. A baby long-tailed macaque (M. fascicularis) pictured. Photograph acquired from Adobe Stock.

Primates obviously do not make suitable pets, particularly as they develop abnormal behaviors in the absence of kin and otherwise enriched environments. Aggression toward unfamiliar people is common in these animals (Soulsbury et al. 2009), and the risk of infection transmission is significant. New World species can transmit Klebsiella and hepatitis A to their owners (Renquist & Whitney 1987), and many pet macaques in the United States harbor cercopithecine herpesvirus 1 (Ostrowski et al. 1998). Despite the risks of ownership, many people still choose to keep primates as companion animals (Figure 3), particularly small monkey species throughout Southeast Asia and South America (Malone et al. 2002). For some people, keeping an exotic species is an indicator of social and economic status, whereas for others these animals are seen as disposable entertainment or even as sources of good luck (Fuentes 2013). Many of these animals are kept for utilitarian reasons, such as pig-tailed macaques (M. nemestrina), which pick coconuts in Thailand (Sponsel et al. 2002). Others are “performance” animals, trained to participate in staged interactions such as with street performers for monetary donations (Ohnuki-Tierney 1987). Performance macaques in Indonesia do harbor retroviruses that could be transmitted to owners as well as to audience members (Schillaci et al. 2005). The “commodification” of primates by humans, despite the risks of pathogen transmission, extends widely (Fuentes 2013).

ANIMALS AS FOOD

Livestock obviously harbor organisms that are pathogenic to humans (Morand et al. 2014). Beyond typical intestinal helminths, protozoa, and bacteria, several other pathogens can be particularly problematic, such as Bacillus anthracis (anthrax), Brucella spp. (brucellosis), Leptospira interrogans (leptospirosis), and Burkholderia pseudomallei (melioidosis) (Weber & Rutala 1999). Consumption of livestock infected with the prion that causes bovine spongiform encephalopathy (mad cow disease) was responsible for variant Creutzfeldt-Jakob disease in the United Kingdom and the
Bushmeat serves as a very significant source of EIDs, even more so than livestock. Bushmeat represents the harvesting of nondomesticated (wild) tetrapods (superclass Tetrapoda: mammals, birds, reptiles, and amphibians) for food, medicine, trophies, and other traditional, cultural uses. For many people (with acknowledged significant variation in cultural habits), bushmeat represents a critical source of protein and household income. It is obtained where domesticated sources are unavailable (Bowen-Jones & Pendry 1999), is often less expensive than domesticated animals (Karesh & Noble 2009), and plays central roles for social traditions in many populations. For very-low-income households, wild game is an important tradable commodity (De Mérode et al. 2003). The widespread use of firearms combined with the development of logging roads and the potential large profit margins of hunting/trapping have facilitated a global trade that has significant impacts on local ecosystems. Displacement of populations into previously undisturbed areas as a result of civil conflict and increased demands due to population growth contribute to overharvesting of wild products. Although it is impossible to clearly understand the scope of the problem, millions of tons of wild-animal meat are sold and consumed annually in West and Central Africa (Chardonnet et al. 2002), with an annual monetary value of at least $200 million (Davies 2002). In the Daobly market of Taï, Côte d’Ivoire, more than 9,000 primates are sold annually as meat, contributing to ~3% annual loss of the general primate population (Covey & McGraw 2014) (Figure 4).

Hunting of exotic species can contribute to animal conservation by generating funds for protecting areas and animals. Many people pay enormous sums of money to put the prizes of their hunts on display in a taxidermic tribute. Yet many of us find it repulsive that the Minnesota dentist Walter Palmer illegally baited and then wounded Cecil, a dominant male lion (Panthera leo) in Zimbabwe (who was part of an ongoing research study), only to kill the animal almost two days later. Similarly, many of us find it difficult to understand how the decision of Namibia’s Ministry of

Figure 4
(a) Olive colobus monkey (Procolobus verus), lesser spot-nosed monkey (Cercopithecus petaurista), and (b) dried chimpanzee (Pan troglodytes verus) carcass at the Daobly market near Taï, Côte d’Ivoire. Photographs by R. Covey.
Environment and Tourism to issue a hunting license for a black rhinoceros (Diceros bicornis) contributes to the conservation of this critically endangered species, at least without observing where the money flows. The continued demand for hunting of exotic species contributes directly to a thriving canned hunting industry where young carnivores (primarily lions) are hand raised, used in tourism at a young age, and then killed for sport as adults (see http://www.cannedlion.org).

Unlike hunting for sport (a relative sign of prosperity), hunting wild animals (particularly primates) for consumption carries with it certain risks of pathogen transmission (Mossoun et al. 2015). Rural villagers in Central Africa report frequent exposure to primate blood and other fluids through hunting and butchering (Wolfe et al. 2004). Although men typically report more hunting than do women, the opposite is true for butchering. Hunting these animals is associated with the risk of biting (Betsem et al. 2011), and accidental cutting can happen during meat preparation. Primate bushmeat contains a high diversity of retroviruses that have been passed onto humans (Voisset et al. 2008, Liégeois et al. 2012), notably simian immunodeficiency virus (the source of HIV), simian T-lymphotropic virus (the source of human T-lymphotropic virus), and SFV.

HIV is a double-stranded RNA virus of the family Retroviridae, subfamily Lentivirus, with different types, groups, subtypes, and viral clusters that all appear to have originated from simian immunodeficiency viruses (SIVs) from sooty mangabeys (Cercocebus atys), chimpanzees (Pan troglodytes troglodytes), and gorillas (Gorilla gorilla) in West and Central Africa (Hirsch et al. 1989, Huet et al. 1990, Gao et al. 1992, Gao et al. 1999, Yamaguchi et al. 2000, Keeler et al. 2006, Van Heuverswyn et al. 2006, Plantier et al. 2009, Ayohua et al. 2013). At least 24 different primate species naturally harbor SIVs (Peeters et al. 2002), and several of these viruses entered the human population on numerous occasions, accounting for the present diversity we see in HIV today. This original HIV epidemic likely began around 1900 in the Democratic Republic of the Congo (Worobey et al. 2008). Whereas the signs of disease from SIV in humans are lacking (Aghokeng et al. 2010), the risk remains for another mutation of SIV into HIV, particularly as primate bushmeat infected with SIVs and other viruses continues to be harvested and traded (and even imported into the United States; Smith et al. 2012).

Although not yet associated with disease in humans (Boneva et al. 2007) or with human-to-human transmission, SFVs are also common in apes and monkeys hunted for bushmeat (Calattini et al. 2007, Betsem et al. 2011). SFVs are widespread, highly genetically diverse, and highly prevalent even among New World monkeys (Muniz et al. 2013, Ghersi et al. 2015). They have been transmitted to people from wild primates through bushmeat [including mandrills (Mandrillus sphinx), Angola colobus monkeys (Colobus angolensis), chimpanzees (P. troglodytes troglodytes), gorillas (G. gorilla), and various cercopithecines (Cercopithecus spp.); Wolfe et al. 2004, Switzer et al. 2008, Mounga-Ondémé et al. 2010, Mounga-Ondémé et al. 2012, Switzer et al. 2012], as well as from bites by pig-tailed macaques (M. nemestrina), Assamese macaques (M. assamensis), long-tailed macaques (M. fascicularis), and rhesus macaques (M. mulatta) in Central and Southeast Asia (Jones-Engel et al. 2008, Engel et al. 2013).

Processing and consuming primate bushmeat also pose a risk of infection from T-lymphotropic viruses transmitted from various species (Vandamme et al. 1998, Calattini et al. 2005, Wolfe et al. 2005b, Zheng et al. 2010, Calvignac-Spencer et al. 2012, Filipponi et al. 2015), and human T-lymphotropic virus I has been implicated in causing leukemia in adults (Gallo 2011). Primate bushmeat preparation and consumption can also result in the transmission of gastrointestinal parasites (Pourrut et al. 2011) and filoviruses such as Ebola virus disease (EBV) (Olival & Hayman 2014, Monroe et al. 2015). Historically, several outbreaks of EBV in Gabon and the Democratic Republic of the Congo were caused by human contact with infected gorilla and chimpanzee carcasses (Muyembe-Tamfum et al. 2012). The latest EBV outbreak began when a two-year-old boy came across an unidentified animal source (possibly a free-tailed bat) in the forests of Guinea in.
December 2013 (Saez et al. 2014). When it was over, the outbreak left more than 16,000 survivors and 11,000 people dead (Baize et al. 2014).

Knowledge about the risks of disease transmission associated with bushmeat does not appear to detract from hunting and preparing these animals (Subramanian 2012, Paige et al. 2015). Despite such knowledge, precautionary measures against infection transmission are rarely used (LeBreton et al. 2006). There simply exists a demand for cheap protein and a preference for wild game over domestic meat (Toledo et al. 2012). In addition, many cultures value fresh, live animal protein over previously butchered or prepared/refrigerated/frozen. These live animals are traded and sold in markets ("wet markets") that bring together diverse species in high densities under relatively poor conditions (Malone et al. 2002, Webster 2004). Several major epidemics have originated from such locations, such as the recent H5N1 avian influenza outbreak (Mounts et al. 1999) as well as the severe acute respiratory syndrome (SARS) coronavirus (Guan et al. 2003).

FUTURE PROSPECTS

Many researchers have already gone to great lengths to provide excellent recommendations on how future emergence of infectious diseases (including in wild, endangered primates; Macfie & Williamson 2010, Gilardi et al. 2015) may be predicted and prevented (Morse et al. 2012). The summary here echoes many of these ideas but more importantly identifies the most immediately relevant solutions. For most of the literature on these topics, there appears to be a focus on pathogen prospecting, trying to identify potential sources of infection, with surveillance of many different human and wildlife populations. Systematic searches should continue to focus on multihost pathogens and other organisms (particularly retroviruses) that have high potential for host shifts. Bacteria and fungi are currently undersampled (Hopkins & Nunn 2007), which should be corrected with new diagnostic techniques that can search for wide varieties of parasitic organisms simultaneously. Reservoir species that deserve continued and intensified monitoring include bats and rodents (given their global distribution and contributions to past outbreaks), livestock (Keesing et al. 2010, Flanagan et al. 2012), animal shelters (Delwart 2012), and primates, of course (Muehlenbein & Lewis 2013).

Where to monitor geographically is important for the allocation of limited resources. More human pathogens are located in lower latitudes in tropical areas (Guernier et al. 2004) where there is also higher general biodiversity (Murray et al. 2015). However, most EIDs have been reported from developed countries, probably reflecting reporting bias due to increased surveillance in wealthier countries (Jones et al. 2008). Measles, mumps, rubella, diphtheria, and other organisms of domestic animal origin likely originated in temperate zones with large human and livestock populations. Yet future EIDs from wildlife are expected to be concentrated in equatorial developing countries (Jones et al. 2008), particularly Central Africa and Amazonia (Pedersen & Davies 2009), and this will markedly be the case for vector-transmitted pathogens (Wolfe et al. 2005a).

Despite past intensive surveillance in addition to dynamic modeling (Lloyd-Smith et al. 2009), not a single pandemic has ever been predicted before it began infecting humans. Even though we have sophisticated systems for identifying and communicating about outbreaks when they do occur (e.g., the World Health Organization’s Global Outbreak Alert and Response Network), responses to these EIDs have been characteristically reactive (Wolfe et al. 2007, Farrell et al. 2013, Gómez et al. 2013). Investment in behavioral measures to prevent outbreaks provides the most parsimonious solutions, and although this may seem simple, cultural change never is. The remediation of EIDs will be accomplished primarily through human behavioral changes rather than through efforts to hunt novel viruses.
At a time when investment in public health services is decreasing, one of the most effective means of preventing disease transmission will be continued and intensified conservation of wildlife habitats (Wood et al. 2012). Although population control of some reservoir species is necessary (Zinsstag et al. 2007), physical separation between humans, livestock, and wildlife reservoirs would be most effective but almost impossible.

Some behaviors surrounding bushmeat must change. It will take more than providing alternative protein sources to decrease many communities’ reliance on bushmeat, so educational sessions on infection prevention during hunting and butchering will prove to be very important (Pike et al. 2010). Risk will always remain as long as there is continued cultural tolerance and preference for wild-animal products. Efforts in biosecurity around livestock operations must be reinforced, and import restrictions on agricultural products from certain areas should be enforced (Marano et al. 2007).

In addition to those involved with bushmeat, other human groups should be intensively monitored as sentinels for EIDs. These include zoo workers, field ecologists (including professional primatologists; Engel & Jones-Engel 2012), tourists (and those traveling internationally for work, even for professional anthropology conferences), military personnel, refugee populations, airline personnel, cruise ship passengers, wildlife filmmakers and photographers, attendees at international field schools, health care workers (particularly veterinarians), sex workers, blood transfusion recipients, and immunosuppressed populations. In particular, focus should be placed on these populations in areas where there is significant overlap with local wildlife populations, such as fragmented, mosaic landscapes as well as wet markets and protected parks.

Anthropologists are in an excellent position to be involved with outbreak prevention by engaging the public, understanding cultural variation in attitudes toward other species as well as perceived risks, and communicating about necessary behavioral changes. Future studies on infectious disease ecology require interdisciplinary cooperation (with global solidarity emphasized over national sovereignty; Heymann 2006), and the results of this work will require effective communication within numerous cultural contexts (Lapinski et al. 2015, Wolf 2015). Successful intervention strategies require an understanding of how disease and public health programs are conceptualized locally. This knowledge will be important particularly for preventing the misgovernance of epidemics and some of the slow public health responses that have occurred in the past (e.g., underreporting of human cases of avian influenza in certain countries; Cyranoski 2005, Normile 2005). Anthropologists can play a critical role in understanding how human health is contextualized relative to both local ecosystem change and general globalization. Education on EIDs must range from basic preventive practices in personal gardens (Mason et al. 2015) all the way up to international enforcement of health regulations (WHO 2005).

Communication about wildlife-associated disease and the interdependence of the health of humans, livestock, and wildlife is a particularly sensitive matter, with accurate public perception necessary for continued support of One Health initiatives (Decker et al. 2012). Fear and otherwise poor reactions to animals as sources of disease will produce undesirable outcomes for wildlife conservation. Miscommunication and inaccurate media coverage [including sensationalism as seen in the movies Outbreak (from 1995) and Contagion (from 2011)] will undermine efforts to empower people to take active roles in disease prevention while respecting the life of wild animals and the places they inhabit. For example, fear of howler monkeys following an outbreak of yellow fever virus in Brazil led to the unfortunate poisoning of many animals (Bicca-Marques & Freitas 2010). Risk communication must be contextualized with messages tailored to different groups so as to temper public concerns. Given the history of human interactions with wildlife, candid discussions about zoonotic EIDs will be increasingly important for our joint survival. The global management of these epidemics is an obligation that transcends any one discipline.
DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

I thank Richard Bribiescas and Karen Strier for the invitation to produce this manuscript, Thad Bartlett, Ryan Covey, Steffen Foerster, and Amy Klegarth for photographs, and Elisha Gray, Martha Lyke, Jennifer Mann, Samantha Mendoza, and Eric Shattruck for assistance with manuscript production.

LITERATURE CITED

Awadallah MA, Salem LM. 2015. Zoonotic enteric parasites transmitted from dogs in Egypt with special concern to Toxocara canis infection. Vet. World 8:946–57


Bowen-Jones E, Pendry S. 1999. The threat to primates and other animals from the bushmeat trade in Africa, and how this threat could be diminished. Oryx 33:233–46


Gómez JM, Nunn CL, Verdi M. 2013. Centrality in primate-parasite networks reveals the potential for the transmission of emerging infectious diseases to humans. PNAS 110:7738–41
Harris NC, Dunn RR. 2013. Species loss on spatial patterns and composition of zoonotic parasites. Proc. R. Soc. B. 280:20131847


Swaddle J, Calos P. 2008. Increased avian diversity is associated with lower incidence of human West Nile infection: observation of the dilution effect. PLOS ONE 3:e2488


Whewell W. 1840. The Philosophy of the Inductive Sciences, Founded Upon Their History. 2 vols. London: John W. Parker


Wolf M. 2015. Is there really such a thing as “one health?” Thinking about a more than human world from the perspective of cultural anthropology. Soc. Sci. Med. 129:5–11


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