EcoHealth
https://doi.org/10.1007/s10393-017-1306-1

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Review

Pathogen Transmission from Humans to Great Apes is a Growing Threat to Primate Conservation

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Abstract: All six great ape species are listed as endangered or critically endangered by the IUCN and experiencing decreasing population trends. One of the threats to these non-human primates is the transmission of pathogens from humans. We conducted a literature review on occurrences of pathogen transmission from humans to great apes to highlight this often underappreciated issue. In total, we found 33 individual occurrences of probable or confirmed pathogen transmission from humans to great apes: 23 involved both pathogen and disease transmission, 7 pathogen transmission only, 2 positive antibody titers to zoonotic pathogens, and 1 pathogen transmission with probable disease. Great ape populations were categorized into captive, semi-free-living, and free-living conditions. The majority of occurrences involved chimpanzees (*Pan troglodytes*) ($n = 23$) or mountain gorillas (*Gorilla beringei beringei*) ($n = 8$). These findings have implications for conservation efforts and management of endangered great ape populations. Future efforts should focus on monitoring and addressing zoonotic pathogen and disease transmission between humans, great ape species, and other taxa to ensure the health of humans, wild and domestic animals, and the ecosystems we share.

Keywords: Endangered, Hominidae, Non-human primates, Zoonoses, One Health, Free-living

Introduction

The family Hominidae includes seven species: humans (*Homo sapiens*), bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), Eastern gorillas (*Gorilla beringei*), Western gorillas (*Gorilla gorilla*), Sumatran orangutans (*Pongo abelii*), and Bornean orangutans (*Pongo pygmaeus*). Six of these species, the non-human primates (NHP), or great apes, have experienced decreasing population trends over the last 40 years (Walsh et al. 2003; IUCN 2016a) (Table 1). Bonobos and chimpanzees are listed by the International Union for Conservation of Nature (IUCN) as endangered; Eastern gorillas, Western gorillas, Sumatran orangutans, and Bornean orangutans are critically endangered (IUCN 2016a, b). By contrast, the human population has increased to 7.6 billion with projections of 8 billion by 2025 and over 9 billion by 2050 (IUCN 2016a). This marked difference in population trends between humans and our closest relatives is primarily caused by anthropogenic threats to NHP, including poaching, habitat destruction, and diseases (Walsh et al. 2003; IUCN 2015; Deem 2016; IUCN 2016a, b).

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Published online: 23 January 2018

Table 1. Available Population Data on All Non-human Primates in the Hominidae Family.

Great ape	Year [source(s)]	Population
Eastern gorilla—Virunga Mountain	1989 (Gray et al. 2013)	325
	2003 (Gray et al. 2013)	380
	2010 (Gray et al. 2013)	480
Eastern gorilla—Bwindi Mountain	2006 (Guschanski et al. 2009)	302
	2011 (Roy et al. 2014)	400–430
Eastern gorilla—Grauer's gorilla	1994 (Plumptre et al. 2015)	16,900
	2015 (Plumptre et al. 2015)	3800
	2054 (Plumptre et al. 2016)[a]	97% projected loss, entire population
Western gorilla—Western Lowland	2013 (Maisels et al. 2016)	18.75% decline, from 2005
Western gorilla—Cross River	2005 (Oates et al. 2003; Sunderland-Groves et al. 2003)	250–300
Bornean orangutan	1973 (Ancrenaz et al. 2016)	2,88,500
	2016 (Ancrenaz et al. 2016)	1,04,700
	2025 (Ancrenaz et al. 2016)[a]	47,000, 82% projected loss from 1950 to 2025, entire population
Sumatran orangutan	2016 (Singleton et al. 2016; Wich et al. 2016)	14,613
	2060 (Singleton et al. 2016; Wich et al. 2016)[a]	80% projected loss from 1985 to 2060, entire population
Bonobo	2015 (Fruth et al. 2016; Sop et al. 2016)	54.9% decline, from 2003[b]
Chimpanzee	2003 (Butynski 2003; Humle et al. 2016)	172,700–299,700
	2050 (Butynski 2003; Humle et al. 2016)[a]	50% projected loss from 1975 to 2050, entire population

[a]Projected.
[b]Estimated—only 30% of the Bonobo population historic range has been surveyed.

The close phylogenetic relationship between humans and other Hominidae species, combined with a rapidly expanding human–animal interface, enables pathogen transmission across species, leading to morbidity and mortality in great ape populations throughout the world (Goodall 1971; Wallis and Lee 1999; Ferber 2000; Woodford et al. 2002; Kaur et al. 2008; Kondgen et al. 2008; Palacios et al. 2011; Deem 2016; Estrada et al. 2017). Several factors contribute to increased interactions between humans and great apes, including civil unrest, ecotourism, human population growth along the borders of protected conservation areas, and the presence of research personnel visiting habituated groups of great apes (Sleeman et al. 2000; Byers et al. 2003; Kondgen et al. 2008; Rwego et al. 2008; Wittemeyer et al. 2008; Gray et al. 2013).

There has been significant research and media coverage of zoonotic diseases that threaten human populations, with many of these having a wild animal reservoir (Kruse et al. 2004; Wolfe et al. 2007; Jones et al. 2008; Quammen 2012, 2014). In contrast, relatively little attention has been dedicated to zoonotic disease events that threaten great ape populations. For example, despite extensive media coverage of the 2014 Ebola outbreak, relatively few people are aware that Ebola has decimated gorilla and chimpanzee populations since 1990, including extirpation of some populations (Huijbregts et al. 2003; Pourrut et al. 2005; Bermejo et al. 2006; Lahm et al. 2007).

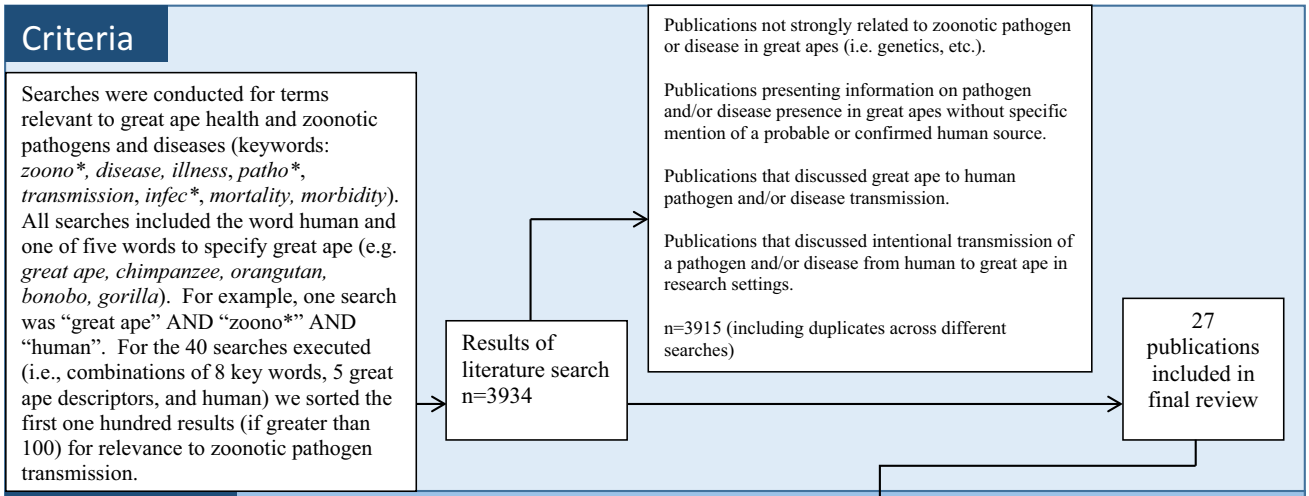
In this paper, we review the literature on pathogen transmission from humans to great apes and explore the effects of disease-causing agents on great ape health and conservation. Factors contributing to pathogen transmission from humans to great apes are discussed, including current issues in public health and conservation. Various terms such as ''reverse zoonoses'' and ''anthropozoonotic''

are sometimes used to describe the transmission of diseases from humans to animals (Wolfe et al. 1998; Wallis and Lee 1999). Throughout this review, we use "zoonotic" to describe pathogen or disease transmission from animals to humans and humans to animals, including occurrences of pathogen and disease transmission, pathogen transmission with probable disease, pathogen transmission only, and positive antibody titers to pathogens (Wolfe et al. 1998; Wallis and Lee 1999).

Methods

We performed word searches using Google Scholar for terms relevant to great ape health and zoonotic pathogens and diseases (keywords: *zoono**, *disease*, *illness*, *patho**, *transmission*, *infec**, *mortality*, *morbidity*) (Fig. 1). All searches included the word human and one of five words to specify great ape (e.g., *great ape, chimpanzee, orangutan, bonobo, gorilla*). For example, one search was "great ape" AND "zoono*" AND "human." For the 40 searches executed (i.e., combinations of 8 keywords, 5 great ape descriptors, and human), we sorted the first one hundred results (if greater than 100) for relevance to zoonotic pathogen transmission. There were no restrictions on species of great apes, geographical areas, or date of occurrence. The literature search was completed in March 2017.

Results were reviewed based on several inclusion criteria. Sources presenting serological studies assessing antibody titers to zoonotic pathogens and case reports or descriptions of zoonotic pathogen or disease transmission affecting an individual or population were included. In each case, we required that authors discussed probable or



	Population Classification		
	Captive	**Semi-Free-Living**	**Free-Living**
Description	well-defined enclosures, human monitoring and intervention: zoos, sanctuaries, research, rehabilitation	habituated for research or ecotourism or reintroduced to the wild after significant human contact or intervention	minimal human contact
Alternative Terms	-	"habituated"	"non-habituated"
Number of Publications	7	19	3
Example Reference	Kooriyama et al. 2013	Palacios et al. 2011	Gracyzk et al. 2002

	Captive	**Free-Living**	**Semi-Free-Living**	**Semi-Free-Living & Free-Living**	**Total**
Chimpanzee, Orangutan, Gorilla	2	0	0	0	**2**
Chimpanzee	4	0	17	0	**21**
Gorilla	1	1	6	2	**10**
Total	**7**	**1**	**23**	**2**	**33**

Fig. 1. Graphical display of methods, from search criteria to population classification through results.

confirmed human to great ape transmission of the pathogen and/or disease. Results presenting information on pathogen and/or disease presence in great apes without specific mention of a probable or confirmed human source were not included. Sources that discussed great ape to human disease transmission or intentional disease exposure to great apes in research settings were also not included.

Great ape populations described by sources included in the final analysis were categorized as captive, semi-free-living, and free-living based on population condition and level/type of human contact. "Captive" great ape populations included animals housed in zoos, rehabilitation centers, research facilities, sanctuaries, and illegal poaching facilities in which they were held in a well-defined enclosure, with some form of human monitoring and interventions. "Semi-free-living" great ape populations were habituated for research or ecotourism or reintroduced to the wild after human contact or intervention such as rehabilitation. "Free-living" great ape populations had not been habituated by humans.

Results

The literature review process identified 27 sources describing 33 occurrences of pathogens in great apes during 1964–2012 with probable (n = 31) or confirmed (n = 2) human origin. These 33 occurrences included instances of pathogen and disease transmission (n = 23), pathogen transmission only (n = 7), positive antibody titers to zoonotic pathogens (n = 2), or pathogen transmission with probable disease (n = 1) (Fig. 2c). Occurrences were found in great apes in captive (n = 7), semi-free-living (n = 25), and free-living (n = 3) conditions, with two occurrences affecting populations in both semi-free-living and free-living conditions. The most represented species/subspecies were chimpanzees (n = 23) and mountain gorillas (*G. b. beringei*) (n = 8), with fewer reports in orangutans (n = 2), a Grauer's gorilla (*G. b. graueri*) (n = 1), and a Western Lowland gorilla (*G. g. gorilla*) (n = 1); two occurrences affected chimpanzees, orangutans, and gorillas (Fig. 2b). We present species affected, population category (captive, semi-free-living, free-living), pathogen or disease, diagnostic modality, morbidity and mortality when provided, date and location of occurrence, and sources (Fig. 2a–d) (Table 2).

Captive

Seven occurrences (21%) were found describing pathogen transmission from humans to great apes in captive popu-

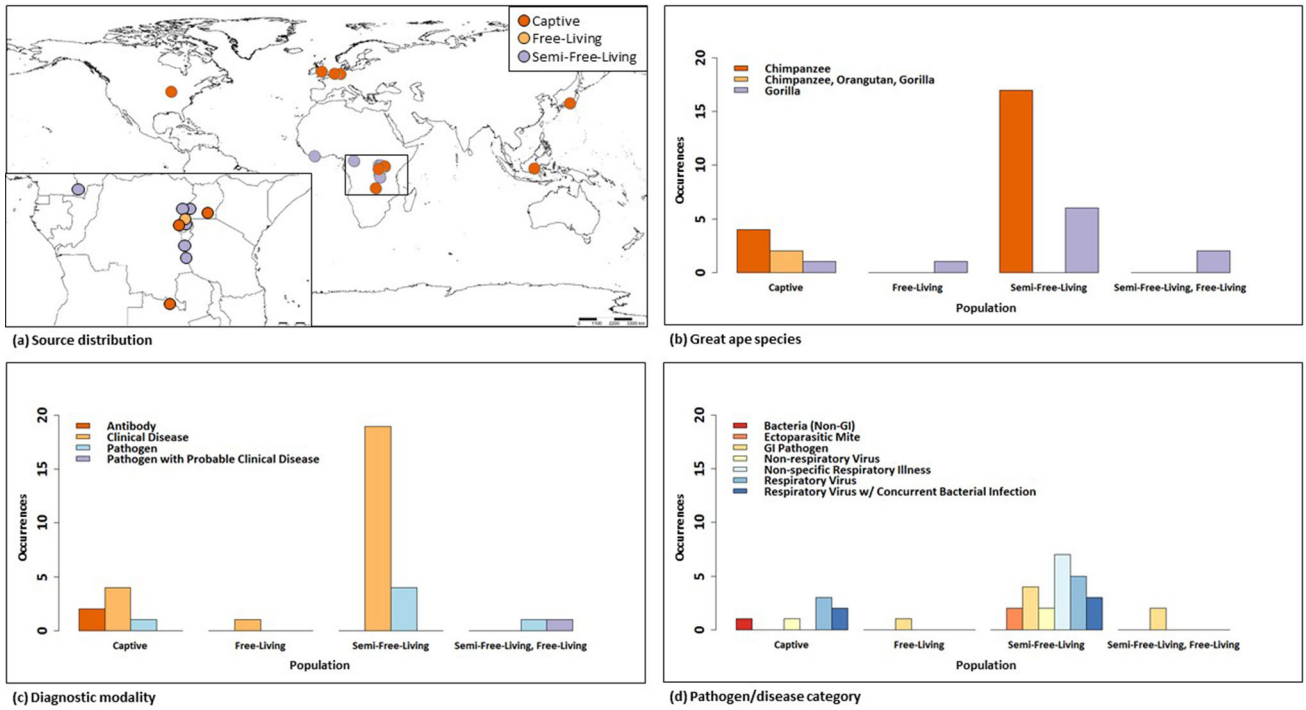


Fig. 2. Reported occurrences of zoonotic transmission from humans to great apes by population. **a** Source distribution, **b** great ape species, **c** diagnostic modality, and **d** pathogen/disease category.

Table 2. Reported Occurrences of Zoonotic Pathogen and/or Disease Transmission from Humans to Great Apes During the Period 1964–2012.

Great ape	Description	Location	Year [source]	Pathogen(s) and/or disease(s)	Diagnostic modality	Morbidity (%)	Mortality	
							(%)	(#)
Multiple species—chimpanzee, orangutan, gorilla (1)	C	Allwetter Zoo, Munster, Germany	2000s (Szentiks et al. 2009)	HRSV, *S. pneumoniae*	Clinical disease	74	4	1
		Biomedical Primate Research Centre (BPRC), Netherlands; Wanariset orangutan Rehabilitation Centre, East Kalimantan, Indonesia; Various zoos	1990s–2000s (Buitendijk et al. 2014)	RSV, hMPV, H1N1 and H3N2 influenza A viruses, influenza B virus	Antibody	–	0	0
Chimpanzee (21)	C	Chester Zoo, UK	2009 (Unwin et al. 2013)	HRSV, *S. pneumoniae*	Clinical disease	100	10	3
		Chimfunshi Wildlife Orphanage, Chingola, Zambia Ngamba Island Chimpanzee Sanctuary, Uganda	2007, 2010, 2011 (Schaumburg et al. 2012)	*S. aureus*	Pathogen	58	0	0
		Kyoto University Primate Research Institute (KUPRI), Kyoto, Japan	2007–2010 (Kooriyama et al. 2013)	RSV, hMPV, H1N1 and H3N2 influenza A viruses, influenza B virus	Antibody	–	0	0
		Lincoln Park Zoo, Chicago, IL	2009 (Slater et al. 2014)	hMPV	Clinical disease	100	14	1

Table 2. continued

Great ape	Description	Location	Year [source]	Pathogen(s) and/or disease(s)	Diagnostic modality	Morbidity (%)	Mortality	
							(%)	(#)
	S	Beni, Democratic Republic of Congo	1964 (Kortlandt 1996)	Polio-like virus	Clinical disease	–	0	0[b]
		Gombe National Park, Tanzania	1968 (Tegner 2013; Wallis and Lee 1999)	Pneumonia	Clinical disease	63	8	5
			1975 (Wallis and Lee 1999)	Pneumonia	Clinical disease	–	–	1
			1978 (Wallis and Lee 1999)	Pneumonia	Clinical disease	–	–	1
			1987 (Tegner 2013; Wallis and Lee 1999)	Pneumonia	Clinical disease	40	17	9
			1966 (Goodall 1971)	Polio-like virus	Clinical disease	–	–	6[c]
			1996 (Wallis and Lee 1999)	Respiratory disease	Clinical disease	–	–	11
			1997 (Pusey 1998)	Scabies: *Sarcoptes scabiei*	Clinical disease	–	–	3
			1989 (Murray et al. 1991)	Ascarid	Pathogen	–	0	0
		Kibale National Park, Uganda	2004 (Goldberg et al. 2007)	*Escheria coli*	Pathogen	–	0	0
		Mahale Mountains National Park, Tanzania	1993 (Hosaka 1995)	Flu-like disease	Clinical disease	–	11	11
			2006 (Hanamura et al. 2008; Kaur et al. 2008)	Human-related metapneumovirus	Clinical disease	35–48	5–19	3[d]
			2005 (Kaur et al. 2008)	Paramyxovirus	Clinical disease	52	3	2
			2003 (Kaur et al. 2008)	Respiratory illness	Clinical disease	98	7	4

Table 2. continued

Great ape	Description	Location	Year [source]	Pathogen(s) and/or disease(s)	Diagnostic modality	Morbidity (%)	Mortality	
							(%)	(#)
		Tai National Park, Ivory Coast	2004 (Kondgen et al. 2008)	hMPV, *S. pneumoniae*, *P. multicoda*	Clinical disease	100	18	8
			1999 (Kondgen et al. 2008)	HRSV, *S. pneumoniae*	Clinical disease	100	19	6
			2006 (Kondgen et al. 2008)	hMPV, *S. pneumoniae*	Clinical disease	92	3	1
Mountain gorilla (8)	S	Bwindi Impenetrable National Park, Uganda	1996 (Kalema-Zikusoka et al. 2002)	Scabies: *Sarcoptes scabiei*	Clinical disease	100	25	1
		Bwindi Impenetrable; Mgahinga National Park, Uganda	1999 (Nizeyi et al. 2001)	*Campylobacter* spp.; *Salmonella* spp.; *Shigella* spp.	Pathogen	19; 13; 6[a]	0	0
		Volcanoes National Park, Rwanda	1995–1997 (Sleeman et al. 2000)	Trichuris trichiura, *Strongyloides* sp., *Oesphagostomum* sp., *Trichostrongylus* sp., Entamoeba histolytica, and *Giardia* sp.	Pathogen	–	0	0
			2009 (Palacios et al. 2011)	hMPV	Clinical disease	92	17	2
			1988 (Hastings et al. 1991)	Measles	Clinical disease	81	10	3
	S + F	Bwindi Impenetrable National Park, Uganda	1990s (Nizeyi et al. 1999)	*Cryptosporidium* sp., *Giardia* sp.	Pathogen with probable clinical disease	11; 2[a]	0	0
		Bwindi Impenetrable National Park, Uganda	2005 (Rwego et al. 2008)	*Escheria coli*	Pathogen	–	0	0
	F	Bwindi Impenetrable National Park, Uganda	2000s (Graczyk et al. 2002)	Giardia duodenalis	Clinical disease	2	0	0

Table 2. continued

Great ape	Description	Location	Year [source]	Pathogen(s) and/or disease(s)	Diagnostic modality	Morbidity (%)	Mortality (%)	Mortality (#)
Eastern gorilla–Grauer's gorilla (1)	C	Goma, Democratic Republic of Congo	2007 (Gilardi et al. 2014)	HSV-1	Clinical disease	71	0	0
Western gorilla–Western Lowland (1)	S	Dzanga Sangha Protected Areas, Central African Republic	2012 (Grutzmacher et al. 2016)	HRSV A	Clinical disease	50	0	0

C, captive; S, semi-free-living; F, free-living; S + F, both semi-free-living and free-living.
[a]Respectively.
[b]0 dead; 7 paralyzed.
[c]6 dead; ≥ 6 paralyzed.
[d]3 confirmed dead; 9 assumed.

lations. These occurrences included positive antibody titers to zoonotic pathogens (n = 2), pathogen transmission only (n = 1), and both pathogen and disease transmission (n = 4) (Fig. 2c). Six occurrences were considered to be of probable human origin, and one study documented an occurrence of confirmed human origin.

A respiratory disease outbreak at the Allwetter Zoo in Germany caused clinical signs in gorillas, chimpanzees, and Bornean orangutans, as well as in three staff members. This outbreak led to the death of a 19-month-old female chimpanzee from pneumonia due to coinfection with human-transmitted human respiratory syncytial virus (HRSV) and *Streptococcus pneumoniae* (Szentiks et al. 2009). Both HRSV and *S. pneumoniae* are known to have a human reservoir, and identical DNA sequences were detected in the chimpanzee and its keeper, suggesting human transmission (Szentiks et al. 2009). A similar coinfection of HRSV and *S. pneumoniae*, the first reported antemortem diagnosis in zoo-housed chimpanzees, affected 30 chimpanzees at the Chester Zoo, UK, leading to three fatalities (Unwin et al. 2013). A human metapneumovirus (hMPV) outbreak in a group of chimpanzees at the Lincoln Park Zoo, Chicago, IL, led to one fatality, with clinical signs of respiratory disease recorded in all seven chimpanzees in the troop. The source of the infection was determined to be of human origin based on prior hMPV seronegative status of all chimpanzees and staff members exhibiting signs of respiratory disease 1 week prior to the outbreak (Slater et al. 2014).

Two serological studies assessed the presence of antibodies to human respiratory viruses in captive great apes. The first tested for antibodies against respiratory syncytial virus (RSV), hMPV, H1N1 and H3N2 influenza A viruses, and influenza B virus in chimpanzees from research facilities, gorillas from zoos, and orangutans from a rehabilitation center. Results showed high seroprevalence to RSV, hMPV, and influenza B virus in all three species as well as evidence of H1N1 infections and low levels of antibodies to H3N2 in many chimpanzees. There were lower levels of antibodies for influenza A and B in the gorilla and orangutan populations compared to the chimpanzees. RSV was found in greater than 70% of both gorillas and orangutans and 96.4% in the chimpanzees' sera (Buitendijk et al. 2014). In the second serological study, 14 chimpanzees were examined for the presence of antibodies to 62 human pathogens. Differences in antibody prevalence were detected for 29 of the 62 human pathogens tested, including a high seroprevalence of hMPV and RSV in over

50% of the chimpanzees and a low seroprevalence against 15 of the tested pathogens, including influenza A (H3N2) (Kooriyama et al. 2013). No antibodies for influenza A (H1N1) or influenza B were found, in contrast to 71.5 and 26.2%, respectively, found by Buitendijk et al. (2014) (Kooriyama et al. 2013).

A bacterial analysis of sanctuary chimpanzees and veterinarians across Africa found multidrug resistant *Staphylococcus aureus* in 58% of chimpanzees and in 33% of humans involved in the study. Most notably, genotype analysis indicated that 45% of positive chimpanzee samples contained isolates from three known human sequence types never previously detected in free-living apes. Additionally, an identical strain was identified in a veterinarian and chimpanzee at one sanctuary, demonstrating direct transmission of a multidrug resistant bacterium from a human to great ape (Schaumburg et al. 2012).

Human herpes simplex virus type 1 (HSV-1) was detected in a juvenile eastern lowland gorilla (reclassified by IUCN as Grauer's gorilla) that had been confiscated by poachers and subsequently housed in a facility in the Democratic Republic of Congo (DRC) with other juvenile gorillas and exposed to a high degree of human contact (Gilardi et al. 2014; Plumptre et al. 2016). An initial presentation of stomatitis, followed by histopathology and molecular screening with sequence analyses, confirmed the presence of HSV-1 in the gorilla. Negative serologic tests suggested this was likely the gorilla's first HSV-1 infection. The HSV infection status of the poachers and subsequent caretakers was unknown, but researchers assumed these individuals were representative of the general population and therefore seropositive, supporting human to gorilla transmission. Regional HSV-1 seroprevalence exceeds 90%, and HSV infections are lifelong (Gilardi et al. 2014).

Semi-Free-Living

Twenty-five occurrences (76%) described pathogen transmission from humans to great apes in semi-free-living populations. These occurrences included pathogen and disease transmission (n = 19), pathogen transmission only (n = 5), and pathogen transmission with probable disease (n = 1) (Fig. 2c).

Five distinct respiratory disease outbreaks involving researchers working with habituated chimpanzees occurred from 1999 to 2006 at Tai National Park in Côte d'Ivoire, with an average morbidity of 92%. Three of these occurrences resulted in fatalities, and *S. pneumoniae* was identified as the most common bacterial pathogen present in necropsy samples screened for respiratory pathogens. HRSV or hMPV was also found in each of the lethal outbreaks, and phylogenetic analysis strongly suggested humans introduced both HRSV and hMPV into these chimpanzee populations. These occurrences include the first direct evidence of virus transmission from humans to non-captive great apes (Kondgen et al. 2008). Additionally, at Volcanoes National Park, Rwanda, a 1988 respiratory disease outbreak attributed to measles virus led to unusually high morbidity and mortality in mountain gorillas (Hastings et al. 1991), and a 2009 respiratory disease outbreak and hMPV infection led to the death of two mountain gorillas (Palacios et al. 2011), both of probable human origin.

More recently, HRSV was detected in semi-free-living lowland gorillas in 2012 the Central African Republic. Three respiratory outbreaks occurred during this time, affecting all eight gorillas of the Makumba group. Fecal samples were collected from each individual in the group, and four gorillas were confirmed positive for HRSV. Sequences from the affected gorillas were shown to be 100% identical to known HRSV A strains. Several humans in the region were also confirmed positive for HRSV. This is the first evidence of HRSV detection in a local human population and habituated great apes with suggested human to great ape disease transmission (Grutzmacher et al. 2016).

Two documented polio-like outbreaks occurred among semi-free-living chimpanzees in Tanzania and the DRC throughout the 1960s (Goodall 1971; Kortlandt 1996). A flu-like epidemic caused the death of at least 11 semi-free-living chimpanzees in Mahale Mountains National Park, Tanzania, in the early 1990s (Hosaka 1995). This group also suffered three respiratory outbreaks in 2003, 2005, and 2006, with the latter two potentially caused by a paramyxovirus and hMPV, respectively (Hanamura et al. 2008; Kaur et al. 2008). Four pneumonia-like epidemics were documented in chimpanzees living within Gombe National Park, Tanzania, from the late 1960s through the 1980s. A lethal polio-like outbreak (11 fatalities, Mitumba group) and an unidentified 1996 respiratory disease outbreak also occurred at Gombe (Goodall 1986; Wallis and Lee 1999).

An ascarid, previously unreported in chimpanzees, was identified in chimpanzees at Gombe, with fishermen who live and work along the shores hypothesized as the human source (Murray et al. 1991). *Escherichia coli* exchange was identified among humans and wild, habituated chim-

panzees in Kibale National Park, Uganda (Goldberg et al. 2007). It was determined that *E. coli* in the chimpanzees was more genetically similar to humans working directly with the chimpanzees, compared to humans from the local village (Goldberg et al. 2007). Antibiotic resistant *E. coli* were collected from 81.6% of the humans and 4.4% of chimpanzees, providing evidence for the transmission of resistant bacteria or genetic elements from humans to chimpanzees (Goldberg et al. 2007).

Cryptosporidium sp. was documented in two populations of habituated Bwindi mountain gorillas with evidence of probable clinical infection in two gorillas, suggesting that the close contact from habituation enhanced pathogen transmission between humans and mountain gorillas (Nizeyi et al. 1999). In fecal samples from habituated mountain gorillas in Bwindi and Mgahinga National Parks, a prevalence of 19, 13, and 6% was determined for *Campylobacter* spp., *Salmonella* spp., and *Shigella* spp., respectively (Nizeyi et al. 2001). In a group of Virunga Mountain gorillas living in Volcanoes National Park, gastrointestinal parasite assessment identified six potentially pathogenic parasites (*Trichuris trichiura, Strongyloides* sp., *Oesphagostomum* sp., *Trichostrongylus* sp., *Entamoeba histolytica*, and *Giardia* sp.); all suggested from human origin (Sleeman et al. 2000).

A study on *E. coli* transmission between humans, mountain gorillas, and livestock in Bwindi Impenetrable National Park found that *E. coli* isolates from a gorilla group habituated for ecotourism were most genetically similar to isolates from humans and livestock, more so than a gorilla group habituated for research. The ecotourism and research groups harbored *E. coli* more genetically similar to the humans and livestock than to the free-living gorillas in the study. The ecotourism group regularly spent time outside of the park boundary with human and livestock contact, while the research group only interacted with researchers. Additionally, it was suggested that transmission of antibiotic resistance from the local human population to the livestock and mountain gorillas occurred (Rwego et al. 2008).

Scabies, caused by *Sarcoptes scabiei*, was documented in habituated Bwindi mountain gorillas with clinical disease in four gorillas and one fatality, an infant male. Humans living in the area had a high prevalence of scabies, suggesting human transmission (Kalema-Zikusoka et al. 2002). A lethal scabies outbreak of probable human origin also occurred in a chimpanzee population in Gombe National Park, causing three fatalities (Pusey 1998).

Free-Living

Three occurrences (9%) in the literature described pathogen transmission from humans to great apes in free-living populations. These occurrences included pathogen and disease transmission ($n = 1$), pathogen transmission only ($n = 1$), and pathogen transmission with probable disease ($n = 1$) (Fig. 2c). All occurrences describe gastrointestinal pathogens in mountain gorilla populations in Bwindi Impenetrable National Park, Uganda. Two studies (Nizeyi et al. 1999; Rwego et al. 2008) also involved semi-free-living animals, described above. In all three studies, water reservoirs, fecal reservoirs, and poor health management of local human populations were considered factors in the spread of zoonotic pathogens between human, livestock, and gorilla populations.

Nizeyi et al. (1999) detected *Cryptosporidium* sp. oocysts and *Giardia* sp. cysts in multiple free-living mountain gorillas, with signs of probable clinical infection. Findings by Rwego et al. (2008) on *E. coli* transmission between humans, livestock, and mountain gorillas showed that *E. coli* collected from a free-living group were least similar to *E. coli* from humans when compared to *E. coli* collected from semi-free-living groups. Despite this, clinically resistant bacteria were identified in the free-living gorillas, suggesting resistant bacteria entered the gorilla population from humans (Rwego et al. 2008).

A 2002 study assessed the presence of *Giardia duodenalis* in Bwindi mountain gorillas (both semi-free-living and free-living), humans who lived or worked there, and cattle with access to the habitat. Two free-living gorillas, three park staff, and five cattle were positive for *G. duodenalis*, and genotypic analysis of bacterial isolates from infected gorillas suggested human origin (Graczyk et al. 2002).

Discussion

Several patterns emerge from this literature review and highlight how occurrences of human pathogen transmission may affect great ape health. The majority of occurrences were documented in semi-free-living populations of chimpanzees and mountain gorillas in protected areas in sub-Saharan Africa. This high number of observed transmissions in chimpanzees and mountain gorillas may be due to greater long-term species' habituation and research efforts, including monitoring of humans and livestock sur-

rounding parks. In occurrences of both pathogen and disease transmission, the majority of studies described respiratory illnesses including pneumonia, HRSV, hMPV, and non-specific respiratory illness, sometimes with concurrent *S. pneumoniae* infection, which occurred exclusively in captive and semi-free-living populations. In instances of only pathogen transmission (i.e., no observed disease) occurring primarily in semi-free-living and free-living populations, gastrointestinal pathogens such as *E. coli* and *Giardia* sp. were more common (Fig. 2a–d) (Table 2).

The occurrences of pathogen transmission in captive settings suggest the need for strict implementation of enhanced biosecurity measures (e.g., facemasks during respiratory disease seasons) and disease surveillance (i.e., preventive medical examinations, regular serological testing), which have been implemented in some cases (Slater et al. 2014). The literature also suggests that the reintroduction of great apes harboring human pathogens and potential transmission to naïve, free-living great apes is a significant issue. These pathogens are difficult to monitor and control and could potentially spread back to local human populations (Schaumburg et al. 2012; Gilardi et al. 2014). Pathogen screening when reintroducing captive great apes into wild populations is a necessary risk assessment (Woodford et al. 2002; Gilardi et al. 2014). Pathogens of particular note that warrant screening based on this review include hMPV, HRSV, and *S. pneumoniae*.

The literature suggests that human habituation of great apes in semi-free-living settings may significantly impact great ape health and conservation through pathogen transmission from humans to great apes. Just as the health of caretakers directly affects the health of captive great apes in their care, the health of researchers, tourists, local villagers, and domestic livestock directly affect the health and survival of semi-free-living and free-living great ape populations and require appropriate biosecurity measures (Wallis and Lee 1999; Woodford et al. 2002; Deem 2016).

The potential risk of pathogen transmission from humans to great apes is compounded by a documented lack of vaccinations in humans living or traveling near great ape habitats (Adams et al. 2001; Guerrera et al. 2003; MGVP 2004). Adams et al. (2001) surveyed the medical histories of both tourists and local villagers at Kibale National Park, home to a number of semi-free-living chimpanzees. Results indicated that many tourists had out of date or missing vaccinations for various diseases including measles (63%), polio (31%), and influenza (97%). Vaccination in the local population ranged from 2 to 70% depending on the disease. Results showed a high prevalence of diarrhea and ongoing infectious disease in the tourists and symptoms of respiratory disease in the local population (Adams et al. 2001). Likewise, the human population surrounding Bwindi Impenetrable Forest National Park was surveyed to determine risks to mountain gorillas living there. The most common symptoms exhibited by humans were cough and fever, suggestive of acute infectious disease. In addition, the survey also indicated a high level of human and gorilla interaction in the area (Guerrera et al. 2003). Among conservation personnel, the Mountain Gorilla Veterinary Project (MGVP 2004) collects health information on the employees of Volcanoes National Park, Rwanda. Analysis of a 2002 dataset indicated that 70.1% (84/120) of employees tested positive for at least one pathogen, and greater than 80% (96/120) had positive viral antibody titers to a zoonotic pathogen, including measles and HSV-1.

Due to the likelihood that in these developing countries, governmental recommendations for vaccinations are not strongly adhered to, it is recommended that personnel and visitors are, at the minimum, tested for tuberculosis and vaccinated against measles and polio (Macfie and Williamson 2010; Gilardi et al. 2015). Vaccination as well as health monitoring of local villagers focusing on clinical signs such as elevated respiratory rates, labored breathing, sneezing, nasal discharge, and coughing is recommended. Additionally, there has been recent discussion of the value of vaccinating non-captive great ape populations for diseases such as ebolaviruses, which have previously devastated great ape populations. We believe that vaccination has the potential for benefit, especially in habituated great ape populations, and it should continue to be a consideration in conservation efforts (Ryan and Walsh 2011; Gilardi et al. 2015; Walsh et al. 2017). There are also mitigation recommendations that focus on the fecal/oral and respiratory droplet transmission routes of these pathogens. Recommendations include IUCN guidelines regarding the proper use and disposal of surgical masks for anyone who will come within 10 m of a great ape, general hygiene and sanitation, and a limit on the daily number of tourists that will visit a great ape group (Macfie and Williamson 2010). These guidelines are freely available to everyone; however, much of the issue lies in the enforcement and consistent use of these guidelines across governments, conservation personnel, tourists, and local villagers (Macfie and Williamson 2010; Gilardi et al. 2015).

Descriptions of disease in non-captive great apes of probable human origin have been available since the 1960s, noting concern for proper management of habituated great

apes for decades (Kortlandt 1996; Wallis and Lee 1999; Woodford et al. 2002). However, as the number of apes habituated for tourism and research has increased, so has local human populations and tourism in these regions, and this may increase the risk of spreading disease (Woodford et al. 2002; Wittemeyer et al. 2008; Macfie and Williamson 2010; Spelman et al. 2013). Faced with consistent environmental and pathogenic threats from expanding human populations, great ape species from captive to free-living may benefit from a One Health approach to manage the present health risks and to mitigate future pathogen transmission (Deem et al. 2001; Deem 2016).

Despite the association of habituation and close human contact with increased disease transmission, there is evidence that some level of human intervention may be required for great ape population growth (Robbins et al. 2011). While the Eastern gorilla species is experiencing a declining population trend, the Virunga Mountain gorilla subpopulation has shown a promising increase in population size (Robbins et al. 2011; Gray et al. 2013; IUCN 2016a). The free-living population, which received only conventional conservation measures, was shown to decline by 0.7% annually from 1967 to 2008 (Robbins et al. 2011), while the semi-free-living population increased by 4.1%, a difference attributed to extreme conservation measures—human intervention, veterinary care, and individual monitoring. Conventional conservation measures, including law enforcement and community development, may minimize negative human impacts and prevent severe population decline but may not adequately support population growth. It is crucial to find the right balance of conservation measures to conserve endangered great apes effectively.

Until the issues discussed above are further resolved, including a lack of vaccinations, improper antibiotic usage, heightened contact between great apes and humans, and shared areas that contain water and fecal reservoirs, humans will continue to be a health risk to semi-free-living and free-living great apes. Without progress, great ape tourism will pose more risks than benefits to habituating great apes (Macfie and Williamson 2010; Gilardi et al. 2015). Progress may be achieved through the use and enforcement of already published guidelines, such as those available from the IUCN (Macfie and Williamson 2010; Gilardi et al. 2015). A One Health approach, including prevention of human to great ape pathogen transmission versus post-pathogen introduction management, may provide a framework for great ape conservation that will not hinder economic growth (Deem et al. 2001; Macfie and Williamson 2010; Palacios et al. 2011; Gilardi et al. 2015).

In conclusion, zoonotic pathogen transmission from humans to great apes is a persistent and growing concern. This is just one of many anthropogenic threats that negatively impact NHP populations, including poaching, habitat loss, and fragmentation. The interconnectedness of human and great ape health must be understood in order to prevent pathogen transmission and spread across taxa. This review of zoonotic pathogen transmission from humans to great apes helps shed light on this underappreciated conservation and health concern. Aggregating and reviewing these data provides conservation practitioners a more thorough understanding of health risks as they work to conserve great ape species and ensure the health of humans, our NHP relatives, and the ecosystems we share.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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