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# Observation of Visitors at a Chimpanzee (Pan troglodytes schweinfurthii) Ecotourism Site Reveals Opportunity for Multiple Modes of Pathogen Transmission

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by

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**3. ABSTRACT**

Chimpanzee *(Pan troglodytes)* tracking is a popular ecotourism activity across Sub-Saharan Africa, offering visitors a personal wildlife experience and providing governments much needed income. However, chimpanzee ecotourism may increase the risk of disease transmission between chimpanzees and people, in both directions, with reverse zoonotic transmission of respiratory pathogens in particular emerging as a major threat to chimpanzee conservation. This study assessed how tourist behaviors might facilitate cross-species disease transmission at a popular tourist site in Kibale National Park, Uganda. We collected observational data during 101 chimpanzee-tracking excursions (n=235 hours). We recorded behaviors of approximately 500 tourists, guides, and student interns. Common behaviors included coughing, sneezing, and urinating, which respectively occurred during 88.1%, 65.4%, and 36.6% of total excursions. Per excursion, individuals touched their faces an average of 125.84 ± 34.45 times and instances of touching large tree trunks or branches averaged 230.14 ± 108.66. These results reveal a diversity of modes by which pathogens might move from humans to chimpanzees directly (e.g. via aerosol transmission) or indirectly (e.g. though the environment or on fomites). Regulations to minimize the impact of ecotourism should consider the realities of tourist behavior and the full range of modes by which pathogen transmission might occur between species.

*Keywords:* Chimpanzees *(Pan troglodytes)*, Primatology, Conservation, Ecotourism, Health and Disease

## 4. LITERATURE REVIEW

### 4.1. Executive Summary

The aim of this literature review is to provide background and rational for studying likely modes of pathogen transmission between humans and wild chimpanzees during ecotourism activities. **Topic I: Chimpanzee Morphology, Ecology & Life History** provides basic knowledge surrounding great ape biology, social structure, and life history, with a particular focus on chimpanzees. **Topic II: Disease**, details the ecology of parasites, viruses, and bacteria most often associated with primates. Case studies are cited to demonstrate the breadth of species and range of research available. **Topic III: Primate Conservation** connects primates to disease, highlighting why zoonotic disease transmission is devastating to both primate and human populations. Within this topic, special attention is paid to respiratory and bacterial infections in chimpanzees. These are the most common types of zoonotic disease and present the greatest threat to chimpanzee populations**. Topic IV: Great Ape Tourism** describes current great ape tourism practices, rules, and regulations. Both the positive and negative side to great ape tourism is presented. Finally, **Topic V: Rationale for Current Study; Conclusion**, clearly states why looking at the most likely modes of pathogen transmission is vital to protecting wild chimpanzee and human populations, protecting the overall biodiversity of primate habitats, and managing primate ecotourism, a very lucrative and necessary source of income.

**4.2. Topic I: Great Ape Morphology and Ecology, & Chimpanzee Life History**

The aim of this topic is to provide basic knowledge about great ape morphology and ecology. Particular focus is paid to chimpanzee (*Pan troglodytes*) life history, humanity's closest living relatives. Understanding them is key to understanding how our shared biology and behaviors can lead to zoonotic disease transmission.

*Great Ape Morphology and Ecology*

Primates are mammals with forward-facing eyes, large brains, and opposable thumbs. These include lemurs, galagos, monkeys, and great apes, including humans (Strier, 2016; Marks, 2017; Larsen, 2018). Great apes have larger bodies, no tails, suspensory adaptations, broad diets, and slow growth histories, meaning long lifespans and low birth rates (Larsen, 2018). Great apes include, gorillas, bonobos, orangutans, and chimpanzees. Chimpanzees are our closest living relatives. Humans split away from chimpanzees between 6-7 million years ago (Strier, 2016). However, chimpanzees and bonobos share approximately 98-99% of their genetic material with humans (Strier, 2016). There are approximately 170,000-300,000 chimpanzees in the wild (Mitani, 2009). There are four subspecies of chimpanzees. *Pan troglodytes schweinfurthii*, are found in 23 countries in equatorial Africa, including: South Sudan, the Democratic Republic of the Congo, Uganda, Rwanda, Burundi, and Tanzania (Muller et al., 2017). In Uganda alone, there are roughly 4,000-5,700 chimpanzees inhabiting both typical wet forests and marginal dry savannah habitats (Muller et al., 2017). However, according to the IUCN (International Union for Conservation of Nature), as the number of mature adults continues to decrease chimpanzees remain on the endangered species list (Larsen, 2018; IUCN, 2019).

Great apes and monkeys have demonstrably different anatomies. Great ape brains are generally larger, relative to body mass than monkey brains, though not remarkably so (Larsen, 2018). Ape brains have more involutions, meaning more surface areas suggesting larger reasoning capacity, larger prefrontal cortices, and novel types of neurons (Marks, 2017; Muller et al., 2017). Their suspensory adaptations include rotating shoulders, long curved fingers, long arms, and short backs (Strier, 2016). These allow for brachiation, arboreal locomotion using the arms to support the body to create a swinging motion. Great apes are diurnal, mostly active during the day and sleep through the night in nests (Strier, 2016). They are also typically frugivorous, or fruit lovers (Strier, 2016). Mountain gorillas being the one exception. Chimpanzee diets are composed of about 60% fruit (Strier, 2016). However, all great apes have flexible diets that respond to seasonal availability (Strier, 2016). Overall, great apes are omnivorous, eating leaves, piths, flowers, shoots, insects, meat, and soil (Strier, 2016).

Knuckle-walking and tool use are two other interesting adaptations within ape populations. Only gorillas and chimpanzees use knuckle walking (Marks, 2017). This is likely because they have exceptionally elongated fingers for suspension, making it difficult and inefficient to walk with flat fingers (Newton-Fischer, 2004; Marks 2017). Orangutans walk on their fists and gibbons, though technically lesser apes usually walk with arms raised (Newton-Fischer, 2004). All great apes can use tools. These include leaf sponges, leaf wipes, and probes (Muller et al., 2017; Marks, 2017). Probes are commonly used to access food sources such as honey and termites, and have been cited in communities in Uganda, Rwanda, and the Congo (Strier, 2016).

Sexual dimorphism is readily apparent in most ape species, usually resulting from competition (Gilby & Wrangham, 2008; Strier, 2016; Larsen, 2018). Males fight for access to fertile females and the larger males usually win. The degree of sexual dimorphism in a species can tell a lot about their mating and social systems. For example, observations that male mountain gorillas are quite large would suggest serious mating competition and that they most likely don't share females (Larsen, 2018). This suggests that mountain gorillas live in small groups with only 1-2 females, which is in fact correct (Larsen, 2018). For chimpanzees, males average 1.3 millimeters tall and 40-60 kilograms in weight, while females average 1.2 millimeters tall and 32-47 kilograms in weight; a 1.2 dimorphism ratio (Strier, 2016). Great ape male canines are also larger than females', though for chimpanzees, not significantly so (Strier, 2016). These characteristics and more, help to make primates a rich, diverse order, teaching humanity about its ancestry and biological history.

*Chimpanzee Life History*

Great apes generally have slow life histories (Strier, 2016). They live long lives, with long juvenile periods, few or single off springs, and long periods between off springs (Sussman et al., 2011, p. 6-20). There is a positive relationship between body size and age of sexual maturity across all mammals (Muller et al., 2017). Bigger animals take longer to grow up. This relationship is exaggerated in primates. Primates have longer juvenile periods than would be expected, and apes have the longest (Sussman et al., 2011, p. 6-20). For example, capuchins take 5-7 years to reach maturity while the average house cat, which is roughly the same size, takes only 9-12 months. Chimpanzees take about 13 years, while dingoes, which are roughly the same size, only take 3 years (Muller et al., 2017).

Infant chimpanzees nurse and are carried by their mothers for about 4-6 years and continue to depend on their mothers until they are around 8 years old (Larsen, 2018). Chimpanzees reach reproductive age around 13-14 years, and most females will leave their natal groups when they reach adulthood (Sussman et al., 2011, p. 6-20). This serves to avoid inbreeding but can be dangerous for the female when approaching a new community (Machanda et al., 2013; Marks, 2017; Larsen, 2018). It is rare, but females can stay with their natal group. This usually occurs when a female's mother is particularly high in the dominance hierarchy (Larsen, 2018). Females produce only one infant every 4-7 years, though twins are possible (Sussman et al., 2011, p. 6-20). When there are twins, usually one will die of exposure (Larsen, 2018). Males reach puberty earlier than females, around 9-11 years old and begin competing for dominance around year 12 (Larsen, 2018). They are considered adults when they enter male hierarchies at around 14-15 years (Marks, 2017). In the wild, chimpanzees can live over 60 years (Strier, 2016; Rowe, 2016).

During mating, female chimpanzees experience obvious ovulation, exhibiting sexual swellings when they are fertile (Marks, 2017). Mating only occurs during fertile periods despite reports that female chimpanzees use mating to leverage food from males (Strier, 2016). Chimpanzees show promiscuous mating behavior. Males attempt to mate with any and all available females and females will mate with any or all males. This allows males to sire as many off spring as possible, and females to confuse paternity to keep offspring safe from infanticide (Marks, 2017). Approximately 1-5% of infant chimpanzees are killed by other chimpanzees (Muller et al., 2017). This is very low compared to gorillas, which have approximately 15% infanticide rate (Muller et al., 2017). Infanticide is a way for males to increase paternity success. After a female's infant dies, she will begin cycling very quickly, so males can copulate with the female when she becomes fertile again. Female cycles last from 30-40 days, but there is a lot of variation between individuals and even between cycles in the same female (Deschner et al. 2003; Strier, 2016; Larsen, 2018).

Chimpanzees have a fission-fusion dynamic. Overall community size can range from 20 to over 200 individuals, so dividing into groups called parties is necessary to avoid food competition (Rowe, 2016). Parties vary in size and composition over time, as individuals come and go due to various circumstances. For example, females have to weigh the cost of grouping with the costs of feeding infants (Marks, 2017). Larger parties tend to deplete food sources more quickly and travel further, so females have to weigh the safety benefit of travelling in larger groups with resource availability (Strier, 2016; Larsen, 2017). Females also tend to be less gregarious, while males spend a lot of time together, have a wider social network, and develop stronger same-sex bonds, all of which can dictate party composition (Muller et al., 2017).

Chimpanzee hierarchy is linear. Males and females have separate within-sex hierarchies and all adult males outrank all females (Byrne, 2007). Males compete for their position in the hierarchy and for direct access to mates. Male position in the hierarchy is reinforced by charging displays, aggression, and pant grunts, as vocalizations of formal submission (Byrne, 2007). The higher a male's position in the hierarchy, the higher the number of copulations (Newton-Fischer, 2004). Therefore, off springs also increase with rank (Wroblewski et al., 2009; Strier, 2016). Within rankings, males form coalitions and alliances. These serve to improve rank, access females, groom more frequently, and are supportive during conflicts. To be in a coalition or alliance with the alpha male is a way to achieve reproductive success, because the alpha will trade access to females for social support (Byrne, 2007; Marks, 2017; Larsen, 2018).

There are sharp differences in social bonds between male and female chimpanzees. Male-male bonds include dominance coalitions, and hunting and territory defense parties (Muller & Mitani 2005; Sussman et al., 2011; Strier, 2016). These bonds are strongest in male-male dyads or pairs (Sussman et al., 2011, p. 6-20). Female-male bonds have intermediate strength and serve as protection and intervention (Kahlenberg & Wrangham, 2010; Sussman et al., 2011; Machanda et al., 2013). Female-female bonds are typically the weakest, most likely due to the costs of feeding and resource competition since most females in chimpanzee communities are unrelated (Larsen, 2018). Grooming is the social glue that serves to help create these bonds, acting as social currency, reinforcing friendships, and reducing risk of tic and other parasitic infection (Sussman et al., 2011, p. 6-20; Strier, 2016; Muller et al., 2017; Larsen, 2018).

When it comes to aggression, males will rarely use force to mate with females, but they do use other forms of coercion such as harassment, intimidation, and coercive mate guarding (Sussman et al., 2011, p. 6-20). Females are more likely to give in to aggressive male mating attempts and some actually approach and solicit copulations from their attackers (Sussman et al., 2011; Strier, 2016). Most often it is the high-ranking males, that are already dominant, who use coercive strategies (Muller et al., 2007; Sussman et al., 2011).

During times of excess energy, usually when there is an abundance of fruit, chimpanzees hunt (Sussman et al., 2011, p. 6-20). Hunting is not frequent but more common in chimpanzees than other primates (Sussman et al., 2011; Strier, 2016). In Uganda specifically, chimpanzees usually prefer to hunt red colobus monkeys, which are known to be aggressive and defensive of their territories (Muller et al., 2017). Different communities of chimpanzees in Uganda have different hunting rates. In Kasekela Community, there were 39 hunts in one year, compared to Kanyawara Community, which had only 5 hunts that same year (Gibly et al., in review). Hunting monkeys is done mostly by males while females capture less risky prey like birds, rodents, and antelopes (Gibly et al., in review). Males share about 40% of carcasses, usually only after harassment (Gibly et al., in review). Most often, males share with other hunters or to show reciprocity to friends. They do not tend to share with females and do not offer meat to females in exchange for copulation (Sussman et al., 2011, p. 6-20; Strier, 2016; Muller et al., 2017).

Chimpanzees use both gestural and vocal commination. There is no evidence of imitative learning of gestures and chimpanzees do not intentionally teach their off springs (Strier, 2016). Chimpanzees are more likely to gesture when their target can see them, but gestures between communities are not always uniform. Scientists at the

University of St. Andrews analyzed over 4,5000 gestures by wild chimpanzees in Uganda to produce a 'dictionary' of 66 intentional hand and body signals used for communication (Hobiter & Byrne, 2014). Some common gestures include: offering a particular part of the body to another as an invitation to groom, stomping of feet to mean 'stop that', tearing strips of leaves with the teeth as flirtation, and showing the sole of the foot to another as an offer for them to climb onto their back (Hobiter & Byrne, 2014). Vocal communication is a closed system with only a certain set of calls, but flexible enough that one vocalization can be used in different contexts (Goodall, 1986; Sussman et al., 2011, p. 6-20; Strier, 2016; Rowe, 2016). There are four categories of vocalizations: dominant, submissive, excitement, and play (Goodall, 1986; Strier, 2016). Dominant vocalizations can include pant-hoots and screams. Submissive vocalizations include pant-grunts, barks, pants, tantrums, but also screams, making context important. The life history of chimpanzees is long and similar to our own. Understanding this supports chimpanzee rights and our need to protect these animals. It also offers insight to behavioral causes of zoonotic disease transmission.

**4.3. Topic II: Disease**

The goal of this topic is to describe and provide examples of parasitic, viral, and bacterial infection in the wild, with a particular focus on primates, as well as highlight epidemiological and immunological factors specific to primates that can contribute to the spread of disease.

*Parasites, Viruses, and Bacteria in the Wild*

Parasites, viruses, and bacteria are living organisms that are ubiquitous. They can be found in water, soil, and even on the surfaces we touch everyday (Harvell et al., 1999). While some bacteria live in and on our bodies not causing us harm, other kinds of bacteria, as well as viruses and parasites, can make us very ill. The difference between the three is that bacteria and viruses can live outside the body, while parasites need a host to survive (Harvell et al., 1999). While antibiotics can destroy bacteria and parasites, they can't kill viruses (Harvell et al., 1999). Viruses are often the cause of respiratory and digestive illnesses. While humans are able to fight off most basic viral infections, most primates cannot, and great apes are particularly susceptible (Kuris et al., 1980).

Habitat loss and hunting are the two most direct causes of primate population decline, but further studies are needed to fully record the impact parasites, viruses, and bacteria have on primate populations, especially in smaller populations that have limited genetic variability. Due to their potential for sudden epidemics and rapid evolution, parasites represent a serious concern in conservation biology (Harvell et al., 1999; Dobson & Foufopoulos, 2001). A formerly healthy ape population in Gabon decreased by 56% from 1983 to 2000 (Tutin & Fernandez, 1984). Distance from the most recent Ebola outbreak explained 63% of the variation (Tutin & Fernandez, 1984). Further research identified Ebola in ape carcasses, while antibodies were present in other primate species in that area, suggesting a particular susceptibility for viral infection in apes (Leroy et al., 2004). Though, primates are not the only order to be impacted by parasitic infection.

Many mammalian species have been brought to the brink of extinction, or extinction, due to parasitic outbreaks. For example, the black-footed ferret (*Mustela nigripes*) was reduced to approximately 20 individuals in a captive breeding program in North America (Lyles & Dobson, 1993). Entire populations of howler monkeys (*Alouatta*) have been exterminated by yellow fever epidemics, and an Ebola outbreak in 2004 eliminated an entire population of 143 gorillas (*Gorilla beringei beringi*) in Lossi Sanctuary (Galindo & Srihongse, 1967; Leroy et al., 2004). It has been suggested that over the last 40,000 years, large mammal extinctions have in part been caused by highly virulent generalist parasites, transmitted by humans and their domesticated animals causing EIDs, emerging infectious diseases (Van Blerkom, 2003).

EIDs in primates and other wildlife have become more of a concern since AIDS, the West Nile Virus, and SARS after having directly impacted human populations (Berger et al., 1998). Previously, EIDs were mostly studied in the global decline of amphibian populations (Berger et al., 1998). EIDs are defined as appearing for the first time, or increasing in prevalence in geographic ranges (Morse, 1995; Daszak et al., 2000; Dobson & Foufopoulos, 2001; Cleaveland at al., 2002; Wobeser, 2002). A large number of EIDs have been noted in mammals including rabies and canine distemper (Scott, 1981; Alexander et al., 1996). EIDs are usually caused by viruses, bacteria, or other micro parasites (Cleaveland et al., 2002). It has been shown that most EIDs can infect a wide range of hosts through cross-species transmission and that habitat loss, pollution, and climate change can enhance the emergence of novel EIDs in wildlife

(Schrag & Wiener, 1995; Daszak et al. 2000; Chapman et al. 2005). For example, bovine tuberculosis infected a wide array of mammals including, wild and captive ungulates, possums, badgers, and chacma baboons (Hunter, 1996; Keet et al., 1996; 2000). Several baboons suffered from rapid disease progression developing lung nodules and emaciation (Keet et al., 2000). In Kruger National Park, one baboon troop reached 50% contamination due to airborne and oral transmission among troop members (Keet et al., 2000). The spread of bovine tuberculosis supports the view that pathogens can travel from reservoir hosts to more susceptible individuals and species.

*Factors that Can Lead to Infection*

In the wild there are many factors that can lead to infection. These factors can be grouped into three categories, individual, social, and geographical variables. Individual variables include: body mass, life history, diet, and individual age. Social variables include: population size, population density, social rank, reproductive status, mating promiscuity, and sex differences. Geographical variables include: range overlap, dispersal, and territoriality, geographic range size, and environmental factors such as seasonality of rainfall and temperature.

Larger primates, those with a greater body mass, are more susceptible to parasites. Being larger, they can provide more niches for parasite colonization and support larger parasite populations (Kuris et al., 1980; Poulin, 1995; Gregory et al., 1996; Poulin & Morand, 2004). In chacma baboons, Pettifer used body mass and age to successfully predict the prevalence and intensity of parasitism (Pettifer 1984). Age suggests that individuals have more time to be exposed to parasites. Hausfater and Watson found that adult male yellow baboons shed more eggs of intestinal parasites than sub adult males, and there were higher rates of schistosome infections in adult than immature baboons (Hausfater & Watson, 1976). Although not all parasitic infections are positively correlated with size and age, many have been, suggesting this to be a substantial link. In regards to diet, greater insectivory, folivory, and omnivory are positively correlated to parasite species richness, prevalence, and intensity (Hausfater & Watson, 1976). However, this could be because species with these particular diets reside in areas with larger parasite numbers and diversity.

Large population size facilitates invasion, leading to increased parasite species richness and prevalence (Hausfater & Watson, 1976). Therefore, parasite diversity and prevalence also increase with population density. If sub structuring occurs in populations, such as parties in chimpanzee communities, the presence of directly transmitted parasites should decrease, but normally increasing group size increases direct parasite transmission (Cheny & Wrangham, 1987). While social behaviors in most great apes result in an inverse relationship between dominance rank and encountering parasites (Hausfater & Watson, 1976), individuals that have higher social ranks are usually groomed more frequently, eliminating parasites from the body. Mating and sex differences can impact STD prevalence and diversity in both males and females, especially in species with promiscuous mating behaviors such as chimpanzees (Hausfater & Watson, 1976).

Geographically, larger ranges increase parasite species richness, and smaller home ranges support opportunities for re-infection (Hausfater & Watson, 1976). This is one reason that chimpanzees usually eat tics and other parasites pulled from the body during grooming. Range-overlap, territoriality, and terrestrial substrate use also affect parasite diversity and prevalence (Watve & Jog, 1997; Wallis & Lee, 1999; Nunn & Altizer, 2006). This is especially true during aggressive territorial actions, particularly in species with well-developed canines such as chimpanzees, able to bite and transfer pathogens, parasites, and other bacteria through contact (Hausfater & Watson, 1976). Environmental factors such as seasonality of rainfall and temperature greatly influence parasite infection (Hausfater & Watson, 1976). Increased rainfall and warmer temperatures increase parasite diversity, prevalence, and intensity (Harvell et al., 1999). Though it is possible that rainfall may wash away some parasites, there is a general trend in wetter habitats, like Kibale National Forest in Uganda, for large parasite populations (Rouquet et al., 2005).

The spread of parasites can even be furthered through predation by means of intermediary hosts. While predation is rarely observed first-hand, field researchers can easily and have often seen species inflicted with intestinal parasites, bot flies, respiratory infections, or other parasitic organism that may be the results of predation (Cheny & Wrangham, 1987). Further studies are needed to understand how predation plays a role in disease transmission.

*Epidemiological and Immunological Factors: Humans as Reservoir Hosts*

Relevant epidemiological and immunological processes related to EIDs (emerging infectious diseases) include parasite establishment in host populations, disease-induced declines or extinctions, genetic changes in hosts or parasites, and how stress and immune defenses impact hosts (Morse, 1995). First, there is the initial introduction of an agent into a novel host population, followed by the establishment and spread at the population level (Morse, 1995). It is stated in the literature that ecological and evolutionary factors of the parasites themselves dictate how successful they will be at infecting a host and potentially spreading to others. If a parasite is able to survive long enough in a host for new mutations to arise, the likelihood of transmission to a new host greatly increases (Schrag & Wiener, 1995). Parasites, viruses, and bacteria can cause both global and local extinctions even at the risk of their own population health (Schrag & Wiener, 1995).

Humans and domesticated animals are important sources of infection for other species because we often exist at high densities and overlap in geographical range. Old World Monkeys and apes are particularly susceptible to infection due to our genetic similarities (Wolfe et al., 1998; Wallis & Lee, 1999; Tutin, 2000; Chapman et al., 2005). Humans and domesticated animals act as reservoir hosts that can infect target host populations. Target host populations are those that parasites, virus, and bacteria can easily infect due to their accessibility and lack of immune defenses. In 1992, Dobson studied the spread of rinderpest in 11 hoofed animal species using nearest neighbor distances to estimate potential within and cross species transmission rates (Nunn & Altizer, 2006). Within rates exceeded cross species transmission rates, but still, these multi-host models can be useful when designing intervention plans to protect wildlife demonstrating the relationship between reservoir and target hosts (Nunn & Altizer, 2006).

Humans are more likely to be reservoir hosts for wild primates, due to our close phylogenetic relationship, especially to apes (Wolfe et al., 1998; Wallis & Lee 1999; Tutin, 2000; Chapman et al., 2005). It has long been known that non-human primates are susceptible to a range of human diseases through biomedical research and a plethora of case studies (Kalter, 1972; Brack, 1987; Chapman et al., 2005). In 2005, Pedersen found that approximately 25% of all micro-and macroparasities reported in wild primates were also reported to infect humans (Pedersen et al., 2005). *Schistosoma mansoni* infections are frequently reported among baboon troops at Gombe, where animals commonly encounter humans (Müller-Graf et al., 1997; Murray et al., 2000). A comparison of baboon populations at Gombe and Mt Assirik in Senegal showed higher levels of intestinal parasites at Gombe (McGrew et al., 1989). In other populations, wild baboons likely contracted tuberculosis multiple times through contact with humans and domesticated animals (Tarara et al., 1985; Sapolsky & Else, 1987; Keet et al., 1996; 2000). Gorillas in the Virunga Mountains are increasingly exposed to infectious material from humans, including food remains, fecal contamination, and even human corpses in the area around Karisoke (Nunn & Altizer, 2006). A measles outbreak in the same area caused the deaths of six female gorillas before a vaccination program could be implemented (Steklis et al., 1997; Mudikikwa et al., 2001). Stuart (1990) found one howler monkey to be infected with the human roundworm (*Ascaris lumbricoides*) living in close proximity to humans. Goodall reported an epidemic of paralysis in chimpanzees at Gombe in 1986 might have been acquired from close contact with nearby humans infected with the polio virus (Goodall, 1986; Wallis & Lee, 1999). Lastly, baboons forging in human garbage dumps were infected with antibiotic-resistant bacteria most likely acquired from humans, and tuberculosis from eating contaminated meat (Phillips-Conroy et al., 1993). Understanding the epidemiological and immunological factors that support humans as reservoir hosts, particularly for primates, helps to construct poignant conservation strategies to protect primates and in turn, keep them from becoming reservoir hosts for future human generations.

*Respiratory and Bacterial Infections in Chimpanzees*

Viral infections in chimpanzees are robust and virulent. What the common cold is to us can easily become deadly for chimpanzees (Muller et al., 2017). Modern humans possess nonrisk alleles implicit to genetically resisting certain viruses such as rhinovirus infections (Muller et al., 2017). Rhinoviruses have been linked to upper and lower respiratory illnesses such as the common cold, asthma, and bronchitis, all of which have caused deaths in chimpanzees (Goldberg et al., 2008).

Epidemic mortality in chimpanzees in Gombe National Park occurred between 1966 and 1997, caused by polio, pneumonia, respiratory disease, and scabies, all mostly likely originating from local people (Wallis, 2000). Additionally, a human researcher was infected by the Ebola virus from a chimpanzee in Cote d'Ivoire in 1994 (Formenty et al., 1999). This suggests that pathogens can travel from humans to chimpanzees and vice versa due to our similar genetic structure, causing serious concern for human health and primate conservation. As mutations occur, chimpanzees can become reservoir hosts for diseases that one day, humans may not be able to withstand. Protecting chimpanzees and other apes from illness is the equivalent to protecting ourselves from disease. The most common types of disease transmitted between humans and wild chimpanzee populations are respiratory illnesses. Even in captive chimpanzee populations in zoos and reserves, deaths due to respiratory illness have been reported and may be higher than literature reports (Gruetzamacher, 2018). The most frequent causes of death are human paramyxoviruses often combined with Streptococcus pneumonia (Nielsen et al. 2012).

Respiratory illnesses in chimpanzees have been a major focus of disease studies. Anthroponotic respiratory pneumoviruses and paramyxoviruses, rhinovirus C, and coronavirus of human origin, have been documented in chimpanzees in western chimpanzees *(Pan troglodyte versues)* in Cote d'Ivoire and eastern chimpanzees *(Pan troglodyte schweinfurthi)* in Tanzania (Negrey et al., 2019). Recently, Negrey (2019) studied two chimpanzee communities in Kibale National Park Uganda, Ngogo Community and Kanyawara Community. Kanyawara is the same community previously shown to harbor E. coli bacteria resistant to certain antibiotics. Two human respiratory viruses were found in each of these communities, human metapneumovirus and human respirovirus 3 (Negrey et al., 2019). Clinical signs and pathologic changes in the infected chimpanzees mirrored those of infected human subjects (Negrey et al., 2019). Infant and older chimpanzees were most directly affected. Human metapneumovirus is similar to a variant that proved lethal to mountain gorillas *(gorilla beringei beringei)*, suggesting that humans or intermediary hosts are the common factor impacting these two great apes. As a result of these outbreaks, 25 chimpanzees at Ngogo died and although there were no deaths at Kanyawara, 69.1% of them exhibited respiratory signs (Negrey et al., 2019). These signs, similar to human symptoms were: coughing, sneezing, dyspnea, lethargy, immobility, and loss of body condition (Negrey et al., 2019). Transmission rates for both communities mirrored those similar to that of the common cold. It should be noted that neither Ngogo nor Kanyawara are tourism communities, that interaction between communities is limited due to territorial behavior, and that trends of illness do occur seasonally with the highest symptoms in March (Negrey et al., 2019). However, due to the frequency of symptoms and the presence of researchers, it is more likely that humans are instigating diseases transmission into these communities through proximity and contact with the environment. Methods to limit these transmissions can protect chimpanzee communities and also serve great benefit to human populations at risk of zoonotic transmission. Proposed methods include, hygiene and sanitation strategies, limited human visitation, and large-scale vaccination of apes (Negrey et al., 2019).

### 4.4. TOPIC III: Primate Conservation

This section has two main themes: disease risk caused by human activities, and current conservation planning and intervention strategies. Human activities include habitat destruction, novel species introductions, and climate change. Conservation planning and intervention strategies include captive breeding, ecotourism, field research, culling, treatment, and vaccination.

*Human Activities*

Primates are the most threatened mammals worldwide with 60% of all species showing evidence for conservation concern (IUCN, 2019; Hilton-Taylor, 2002). Due to habitat fragmentation, non-human primates are likely to come in contact with humans more often. This fragmentation has both positive and negative effects for disease control. On the positive side, smaller fragments work to isolate disease before becoming epidemics, similarly to how subgroups can mitigate the spread of disease within an entire community (Watve & Jog, 1997; Wilson et al., 2003). However, habitat fragmentation increases edge effects, exposing individuals to novel pathogens, introducing them into their population (Cowlishaw & Dunbar, 2000). For example, Chapman (2005) found that two colobinae in Africa were more likely to be infected with multiple species of gut parasites than monkeys on the interior of the fragments. Edge effects can also be caused by road building to hunt or extract forest resources as well as political instability leading to human migration.

Migrations can result in greater population densities potentially increasing the spread of disease (Chapman et al., 2005). Eventually dense populations wither away either by disease or because they're unable to be sustained based on the resources available in limited space (Nunn & Altizer, 2006). Increased population density also results in increased amounts of fecal matter that could lead to contamination. Crowded individuals are also more likely to have higher levels of stress and therefore greater susceptibility to infection and aggression (Nunn & Altizer, 2006). In a semi-captive colony of mandrills, simian immunodeficiency virus (SIV) frequently spread through male-male aggression (Nerrienet et al., 1998). As habitat degradation and fragmentation continues to be caused by human activities such as migration, logging, and farming, population densities will continue to rise.

Populations that are too small can lead to limited genetic diversity. Limited genetic diversity prohibits individuals from fighting off parasites and infectious diseases (Nunn & Altizer, 2006). Smaller population sizes can also lead to inbreeding which has been shown in species such as lions and cheetahs to be directly linked to mortalities (Nunn & Altizer, 2006). It has also been seen that some parasites themselves cause limited genetic variability (O'Brien & Everman, 1988). It can be argued that since hosts eventually die from their parasites, by allowing hosts to die in a way that prohibits transmission, it's possible to eliminate all naturally occurring parasites in an area, saving future populations. However, removing all parasites also removes resistance. It is best to maintain resistance in populations to combat epidemic outbreaks, while also keeping record infection to prepare for possible epidemics.

Human activities such as hunting and butchering meat are a likely avenue of transmission (Rouquet et al., 2005). Chimpanzee meat and bush meat is butchered, sold, and consumed, directly spreading disease (Wolfe et al., 2004). In Cameroon, individuals with high levels of contact with non-human primate body fluids were found to be infected with non-human primate retroviruses and simian foamy viruses, probably contracted during hunting or butchering (Wolfe et al., 2005). However, there are more indirect modes of pathogen transmission through research and chimpanzee ecotourism.

Kibale National Park in Uganda, is a mid-altitude forested park, 795 $km^2$, home to 10 chimpanzee communities 3 of which are used for research and tourism: Ngogo, Kanyawara, and Kanyanchu. At both Kanyawara and Kanyanchu, E. coli isolates were genotyped from fecal samples and results indicated that chimpanzees in Kibale National Park harbored bacteria more genetically similar to bacteria found in humans engaged in research and tourism, than bacteria found in people who lived nearby, with minimal chimpanzee interaction (Chapman et al., 2005). Clinically resistant isolates were also found in chimpanzee fecal samples; despite the fact the chimpanzees were ever administered antibiotics (Chapman et al., 2005). This proves that resistant bacteria or resistance-conferring genetic elements were transferred from humans to chimpanzees most likely through fecal matter or contact with environmental factors (Chapman et al., 2005). Chimpanzees have been known to venture into human villages, and people enter forests to obtain resources, as well as the researchers, tourism employees, and tourists who track chimpanzees on a daily basis. Chapman (2005) suggests that by discouraging defecation in the forest, washing hands before and after entering the forest, and placing distance limits on humans watching chimpanzees, we could help lessen the likelihood of bacterial transmission.

An important impact to note is the effect of humans on parasites themselves, particularly via climate change. Rising temperatures and increased rainfall increase parasitic abundance through greater reproduction and lower mortality rates, which in turn allows them to spread into new geographical locations (Dobson & Carper, 1992). Other human activities such as logging can directly impact mosquito communities and shift the abundance of pathogens they carry (Patz et al., 2000). Many pathogens are directly affected by latitude and longitude, leading to shifts in geographic presence as global temperatures rise. Since many of the biodiversity hotspots where non-human primates live are located near the equator, there is a greater change of infection as temperatures rise and pathogens multiple (Myers et al., 2000). There are also a number of diseases spread through water, such as cholera, which could respond to changes in temperature and water level. Boesch and Boesch-Acherman (2000) found that even Ebola responds to seasonal patterns, more common during exceptionally dry years, as reservoir hosts accumulate in density. It is possible that with increased temperatures and rainfall, some parasites and bacteria will die off, exposed to warmer temperatures, but overall, climate change complements a rising risk of infection and disease transmission (Boesch & Boesch-Acherman, 2000).

*Conservation Planning and Interventions*

Direct intervention, ecotourism, field research, captive breeding, semi-free ranging, reserves, and monitoring parasites in wild populations are current conservation strategies to contain or eliminate infectious disease risk (Nunn & Altizer, 2006). Unless directly related to human health, diseases are not often studied in wild populations. Baboons, chimpanzees, gorillas, and macaques are the most frequently studied species for disease control. A global mammal parasite database has been funded by The National Science Foundation, The National Center for Ecological Synthesis and Analysis, and the Center for Applied Biodiversity Science. This database synthesizes records of parasites and their hosts in all mammalian species from published scientific literature. This database states that over 400 parasite species in total have been reported across all wild primates (www.mammalparasites.org; Nunn & Altizer, 2006). Many of these reports come from biomedical research, and although 400 may seem like a large number, the number of parasites that can infect non-human primates and possibly humans, is well over 400. In humans alone, the database shows over 1,400 parasites that can infect humans, and how many can also infect non-human primates is still unknown (Nun & Altizer, 2006). Screening programs and continuing to develop databases such as this can aid our understanding of where cross-species disease transmission overlaps.

Captive breeding and semi-free ranging interventions can be useful in controlling the spread of disease. Often reserves and rescues are designed after a species is already showing signs of extinction or endangerment. However, surveillance and control of infectious diseases inside parks and breeding facilities is an important component in captive breeding programs and can help isolate an infection before it has a chance to spread, especially when veterinary care is a part of the management plan (Nunn & Altizer, 2006). Captive environments can speed to the spread of disease since animals are kept in relatively close proximity and are already in few numbers when entering such breeding programs, but veterinary care should supplement that issue. Planned releases also harbor the threat of exposing pathogens to wild populations. For example, a plan to reintroduce rehabilitated orangutans in Indonesia was they were found ill with human tuberculosis (Ballou, 1993). This would have been devastating not only for the individual orangutans, but for the habitat into which they were about to be release. Translations offer the same risks, and as habitat destruction continues, translocations are becoming less of a viable option. Screenings, vaccinations, quarantines, reproductive experiments, and medications have all been suggested as ways to manage captive and semi-captive programs (Ballou, 1993; Lyes & Dobson, 1993;

Cunningham, 1996; Mikota & Aguilar, 1996). In the end, translocation on an expedited time scale presents the least opportunity for individuals to be infected with novel hosts and for a smooth re-introduction into a suitable environment (Cunningham, 1996).

Field researchers may introduce infectious diseases during habitation, capture, or simply by living near or in a reserve (Wallis & Lee, 1999). Specific infectious agents that can be transmitted in only a moment of contact with a wild animal or its environment include: shigella, trichuris, hepatitis A and B, herpes simplex, scabies, a variety of intestinal worms, measles, and polio (Homsy, 1999; Wallis & Lee, 1999; Rothman & Bowman, 2003). Outbreaks of measles, human tuberculosis, and influenza have all been found in primates and are most likely due to human contact and vicinity (Wallis & Lee, 1999). Respiratory illnesses are particularly dangerous as gorillas in Volcanoes National Park, Rwanda and Chimpanzees in Gombe have been highly impacted, most likely by researchers and tourists wanting to see these great apes (Goodall, 1986). Tourist and field researcher impact on great apes and other species can be as obvious as directly feeding wild animals. In Gibraltar, despite numerous signs warning tourists to not interact or touch wildlife, tourists have caused human-initiated contacts with a colony of Barbary macaques (*Macaca sylvanus*), at a rate of 44 times per hour with the majority involving direct contact (O'Leary & Fa, 1993). These interactions resulted in lacerations to humans as well as a viral epidemic that hit the macaque population in 1987 resulting in the death of all infants (O'Leary & Fa, 1993).

Direct interventions to mitigate infectious diseases are through vaccinations, culling, and veterinary treatment. For example, researchers in Gombe provided medical attention to chimpanzees in Gombe (Goodall, 1986). Primates are often captured using darts and general anesthetic. Sleeman (2000) summarized 26 surgical procedures performed on over 24 gorillas in nearly 10 years to treat those caught in snares. Overall, these instances have been successful and were required and executed only in dire situations. Vaccinations are more widely used to control infectious disease. In primates, polio vaccinations have been administered to chimpanzees and measles vaccines in gorillas (Goodall, 1986; Sholley & Hastings, 1989). Oral vaccines for such diseases as rabies have also seen to be successful and reduce the need for capture (Sholley & Hastings, 1989). Vaccines and culling have been used to slow the spread of disease or constrict it to a smaller reservoir group that can then be monitored and potentially treated. There are obvious benefits but also detriments to vaccinations including building resistance strains and stress from capture. All conservation planning and intervention strategies must be managed on a case by case basis. There are no definite rules as diseases change and situations vary.

**4.5. TOPIC IV: Great Ape Tourism**

Ecotourism is a popular conservation strategy worldwide that offers tourists the opportunity to learn from and engage with nature. It also provides a source of income that can be used to further conservation efforts and support environmentally friendly programs and initiatives. When safely administered, ecotourism serves a great benefit to both visitors and hosting institutions. However, ecotourism can also pose serious threats to disease control, biodiversity, and environmental education. Negative outcomes are usually due to poor management, political complications, lack of funding, or a lack of knowledge, resources, or communication (Nunn & Altizer, 2006).

Although ecotourists are often environmentally minded, the fact they come from many distant countries provides opportunities for pathogen spillover from international travelers that collectively carry a wide diversity of infectious diseases (Nunn & Altizer, 2006). For example, Adams (2001) conducted a medical history survey of tourists and residents in Kibale National Park, Uganda, home to the Kanyanchu, Kanyawara, and Ngogo chimpanzee communities. Histories were self-reported and results listed the diseases chimpanzees were most likely to come into contact with based on tourist nationalities and travel histories. There was a total of 62 tourist surveys returned, most indicating a high prevalence of disease symptoms, especially diarrhea and a lack of required vaccinations (Adams et al., 2001). The 50 surveys returned from locals showed a high prevalence for symptoms of respiratory illness (Adams et al., 2001). There may be other causes for symptoms unrelated to disease, such as the stress of travelling, and locals usually have minimal contact with chimpanzees, but these surveys suggest further screening measures may be needed to prevent infected individuals from impacting chimpanzee health.

There are six general categories to reduce the spread of infectious diseases in most primate populations. 1) Restrict contact with humans by limiting the number of tourists and researchers that visit a group per day and enforcing minimum approach distances and eliminating feeding opportunities. 2) Prevent sick tourists and researchers from going into the field. 3) Provide emergency contingencies for diseases outbreaks such as veterinary assistance and vaccines. 4) Eliminate contact between wild primates and human waste. 5) Provide a buffer between groups visited by tourists and other wild groups. 6) Ensuring that park staff enforces these rules (Nunn and Altizer 2006).

The International Union for Conservation of Nature (IUCN) is the world's leader in finding pragmatic solutions to pressing environmental and developmental challenges. Established in 1948, they are the world's oldest global environmental organization, present in 160 countries. Their latest Best Practices Guidelines for Health Monitoring and Disease Control in Great Ape Populations was published in 2015 (Gilardi et al., 2015). These guidelines summarize the best practices for disease prevention, health monitoring and disease surveillance strategies, and clinical interventions, all associated with great ape conservation.

A summary of best practices according to the IUCN, in regards to great ape ecotourism is as follows. Pre-visit recommendations include: a minimum age of 15 of all people visiting great apes; ill people should be prohibited from visiting; all people who will be in frequent close proximity, within 10 meters but no closer than 7 meters, should be immunized according to the local government's recommendations for childhood vaccination and should be tested for tuberculosis every year; all foreign visitors who intend to spend extended periods in close proximity to great apes, such as researchers and veterinarians, should be quarantined for at least 7 days before setting foot into a great ape habitat (IUCN, 2019).

During visits: time and contact with great apes should be minimized, the standard time for tourists is one hour; everyone visiting great apes should be wearing clean clothes; footwear should be washed before and after entering a great ape habitat; everyone visiting great apes should sanitize their hands before and after entering a great ape habitat; all visitors should maintain a distance of at least 7 meters from great apes at all times to reduce the risk of pathogen transmission; clean and un-torn facemasks should be wore by all visitors coming within 10 meters of great apes; sneezing and coughing should be done while wearing a facemask and turned away from the apes into the crook of an elbow; to urinate visitors should move at least 100 meters away from great apes and dig a hole at least 30 centimeters deep; defecation should be prohibited in great ape habitats but if it occurred, all feces and waste should be bagged and removed from the forest.

Although IUCN regulations and the categories surrounding great ape safety are clear and concise, disease transmission continues to be a serious threat to wild great ape populations, biodiversity, and human health. This suggests that further research is needed to discover why and how transmissions are continuing to occur. Ecotourism is an exceptional opportunity to teach the public about wildlife conservation, disease control, and overall environmental education. It is not an activity that should be cast aside. However, it may be necessary to update IUCN regulations for the harsh realties some countries face when trying to implement ecotourism programs and take into account the changing body of literature on disease ecology.

### 4.6. TOPIC V: Rationale for Current Study; Conclusion

This topic presents reasons why further study, specifically on the modes of pathogen transmission between humans and wild chimpanzees is necessary. We focus on the impact zoonotic disease transmission is having on human populations today, as well as current gaps in the literature. We hope this study will be used to augment and introduce regulations for great ape tourism activities so that ecotourism can continue to be an educational and lucrative strategy for primate conservation management.

*Impact on Human Populations*

Studying disease in non-human primates has a direct impact on human health care. Most human EIDs (emerging infectious diseases) are viral and can cross the boundaries between species, including HIV/AIDS, SARS, Ebola hemorrhagic fever, and hantavirus pulmonary syndrome (Garret, 1995; Galvani, 2004). Taylor (2001) discovered that more than 60% of human pathogens can be shared with animal hosts. Understanding factors that affect disease in wildlife is increasingly important as human populations expand and migrate, coming into contact with more and more wildlife.

Understanding the distribution of zoonotic diseases and their likely modes of transmission can protect humans now and in the future from primate cross-species contamination as humans continue to invade natural primate habitats. For example, human AIDS can be caused by any 1 of 4 strains of HIV that evolved from SIV (simian immunodeficiency virus) (Watanage, 2004). HIV-1 was most closely related to chimpanzee HIV and HIV-2 is similar to SIV from sooty mangabeys *(cercocebus atys).* SIV has been evolving and entering human populations since 1930, but investigation was only made a priority after human populations started to become infected (Hahn et al., 2000). Humans can be infected with other primate derived viruses such as, simian foamy virus (SFV) and HTLV-3, previously never seen in humans (Wolfe et al., 2005). It is clear that transmission can occur through close contact via biting and scratching, as well as through bodily fluids when primates are hunted and butchered for sale and consumption (Hanh et al., 2000). It is also possible for humans to become infected from handling primate carcasses, infectious stages found in the environment, and via mosquitoes and flies that feed on infected wild primates (Hanh et al., 2000). These avenues are common for tourists, field workers, loggers, and residents near or inside areas inhabited by wild primates, but others can become infected through travel or by means of reservoir hosts long after the initial contamination occurred. Humans are threatened by EIDs, and understanding where they come from and how they spread, is key to protecting our future.

*The Need for Further Research*

Although there is a plethora of information documenting disease outbreak and transmission in on-human primates, few studies have been done on fomites and surface areas as a means of cross-species disease-transmission. Fomites are materials such as clothing and shoes that can harbor pathogens for long periods of time and be transmitted simply by contact (Edemekong & Huang, 2019). It is well known that pathogens can survive on surfaces long after they're deposited (NHS, 2018).

According to the NHS (National Health Service, 2018), cold viruses can survive on surfaces for more than 7 days. Viruses can survive even longer on non-porous surfaces, such as stainless steel or plastics. The ability for a virus to cause an infection rapidly decreases over time, but thinking of activities such as ecotourism, if one person touches over a dozen different surfaces in a forest, and then a vulnerable animal touches even one of those areas in the next week, it could become infected and unable to fight off human strains of a virus it has never been exposed to. Common cold-causing viruses, rhinoviruses, for example, are still infectious on a person's hands after an hour (NHS, 2018). Rhinoviruses are easily combatted by the human immune system, but for species such as chimpanzees that don't have the genetic ability to fight the common cold, they could easily develop more serious infections such as bronchitis or pneumonia, which may result in death. Respiratory syncytial virus (RSV), which is even deadly to humans, can survive on clothing and tissues for 30 minutes and on skin for up to 20 minutes (NHS, 2018). Although this may seem like a short amount of time, other species exposed to this virus only need a moment to become infected. In addition, flu viruses can survive on surfaces for up to 24 hours, and can survive as droplets in the air for several hours (NHS, 2018). Low temperatures, like those during rainfall can increase flu virus survival rates (Edemekong & Huang, 2019). Some germs that cause intestinal bugs include E. coli and salmonella, and can survive on soft fabrics for as long as 5 months and have shown to spread through cross-species contamination (Rwego et al., 2008). For example, samples were taken from humans, livestock, and mountain gorillas *(Gorilla beringei beringei)* in Bwindi Impenetrable National Park, Uganda. It was shown that gorilla populations that overlapped their habitat use with humans and livestock harbored E. coli that was genetically similar to those that could infect people and livestock (Rwego et al., 2008). Additionally, the proportion of gorillas that were clinically resistant to at least one antibiotic used to treat E. coli increased as degrees of habitat overlap increased (Rwego et al., 2008).

The norovirus can be spread by someone who coughs or vomits, and distributed through small droplets in the air, settling on surfaces and remaining for weeks (NHS, 2018). These and other infectious diseases have the lasting power to infect numerous species in a dense forest environment in a short amount of time. It is also common for humans to be infected without symptoms and spread illnesses unknowingly (Edemekong & Huang, 2019).

By studying fomites and likely modes of pathogen transmission in the forest, it is possible to construct conservation strategies that are directed at the most likely pathways of transmission. It is unrealistic to try and eliminate all disease from a forest environment, especially one in which humans reside or border, but knowing the most likely or frequent modes of transmission is a necessary starting point to prevent future disease transmission as well as human and non-human primate mortalities.

## 5. POTENTIAL FOR DISEASE TRANSMISSION AT A CHIMPANZEE ECOTOURISM SITE

### 5.1. Introduction

Ecotourism is a popular and potential conservation activity that offers tourists the opportunity to learn from and engage with nature (Gallagher & Hammerschlag, 2011; Milcu et al., 2013; Chiu et al., 2014; Blumstein et al., 2017). It also provides a source of income that can be used to further conservation efforts and support environmentally friendly programs and initiatives (Weaver, 2001; Clements et al., 2016). When properly overseen, ecotourism can benefit visitors, local communities and hosting governments (Stonza & Durham, 2008). However, ecotourism can also have negative consequences to the plants and animals that tourists visit (Weaver, 2001; Honey, 2002; Rai, 2011). One negative consequence of ecotourism is the transmission of infectious diseases, either from tourists or from tourism-associated personnel (Lim et al., 2018; Palaccios et al., 2018). Such “reverse zoonotic” or “anthroponotic” transmission has been blamed for outbreaks of Middle East respiratory syndrome (MERS), Hepatitis E virus (HEV), and Rift Valley fever (RVF) in African and Middle Eastern countries (Pavio et al., 2010; Arabi et al., 2017; Fawzy et al., 2019)

Reverse zoonotic disease transmission is a particular concern for great apes, which are popular subjects of tourism and are also physiologically similar to humans (Dunay et al., 2018). Dunay et al described 33 occurrences of probable or confirmed pathogen transmission from humans to great apes from 1962-2012 in captive, semi-free, and free-living environments. These occurrences lead to the deaths of 82 individual great apes. In Kibale National Park, Uganda, one of Africa's most popular chimpanzee tourism destinations, Adams (2001) conducted a medical history survey of tourists and residents. Most tourists self-reported recent disease symptoms that could indicate a risk of disease transmission to chimpanzees, including diarrhea and respiratory symptoms, and many also noted a lack of required vaccinations (Adams et al., 2001). Rules set out by government agencies in Uganda include preventing sick tourists and researchers from going into the field, maintaining proper distance from apes, and controlling the duration of ape viewing (Sandbrook & Semple, 2006; Cranfield, 2008; Gilardi et al., 2015; Hanes, 2018), such that these findings indicate room for improvement.

While self-reported survey methods can be useful in some respects, individuals could underreport illnesses or symptoms. Furthermore, some infections are not transmitted directly but instead through fomites, which are inanimate objects that can harbor pathogens and transmit them by subsequent contact (Edemekong & Huang, 2019). According to the National Health Service (NHS, 2018), certain "common cold" viruses can survive on surfaces for more than 7 days. Rhinoviruses, for example, are among the most prevalent such viruses in people worldwide and remain infectious on a person's hands after an hour, and some bacteria that cause gastrointestinal illness including *Escherichia coli* and *Salmonella typhimurium* can survive on soft fabrics for as long as 5 months (Heaney et al., 2009; Garira et al., 2014; Esteves et al., 2016; Greene et al., 2018; Dawley & Gibson, 2018).

Respiratory illnesses have caused significant mortality in African great ape populations, all of which are endangered (Spelman et al., 2013; Davis et al., 2015; Hoppe et al., 2015; Emery Thompson et al., 2018). These illnesses have been implicated in chimpanzee deaths in Tanzania, Democratic Republic of Congo, Côte d'Ivoire, Guinea, and Uganda, for a total of 84 individual deaths of wild chimpanzees from 1968 to 2013 (Leendertz et al., 2004; Calvigna-Spencer et al., 2012; Dunay et al., 2018; Emery Thompson et al., 2018). Agents that can cause respiratory illness in chimpanzees, apart from human contact and proximity, include provisioning, seasonal patterning, and the role of other species, all of which cannot be discounted as potential modes of respiratory disease transmission (Negrey et al., 2019).

In the Kanyawara Community in Kibale National Park, Uganda, respiratory illness has been the leading cause of death for over 31 years (Emery Thompson et al., 2018). The most frequent human-origin etiologic agents responsible for mortality in chimpanzees are RNA viruses of the family Paramyxoviridae (Kondgeni et al., 2017), often with coinfection by *Streptococcus pneumonia* or *Pasteurela* spp. bacteria (Grutzmacher et al., 2018; Kondgeni et al., 2017). Rhinovirus C has also been linked to upper and lower respiratory illnesses in people and mortality in wild chimpanzees (Scully et al., 2018), and other viruses such as human respiroviruses (Scully et al., 2018) and coronaviruses (Patrono et al., 2018) cause milder disease in chimpanzees. Epidemic mortality in chimpanzees in Gombe National Park occurred between 1966 and 1997, caused by polio, pneumonia, respiratory disease, and scabies, all most likely originating from local people (Wallis, 2000).

Unfortunately, the precise modes by which infectious agents are transmitted from humans to wild great apes during ecotourism and similar activities are not well studied. Recent findings have primarily focused on airborne pathogens and direct contact as a means of zoonotic disease transmission. Direct contact includes acts of aggression, as well as human activities such as provisioning and hunting, where people are at high risk of direct contact with infected bodily fluids like blood and saliva (O'Leary & Fa, 1993; Gessain, 2013). However, airborne pathogens are the most widely considered mode of zoonotic disease transmission (Keet at al., 2000; Salem et al., 2019; Manuel et al., 2019; Brown et al., 2019). Petrono et al (2018) reported on an outbreak of human coronovirus (OC43) in chimpanzees living in the Tai National Park, Cote d'Ivoire, focusing solely on airborne pathogens. However, he also states that asymptomatic shedding and seasonal factors cannot be discounted as sources of infection (Petrono et al., 2018). Overall, there is a lack of research exploring exactly how infectious agents are transmitted from human to wild great apes and by studying human behaviors during ecotourism and similar activities; we gain insight into potential modes of transmission.

The objective of this study was to record human behavior during tourism activities that might affect the risk of disease transmission from people to chimpanzees. In Uganda, the Kanyanchu Community of chimpanzees is visited by approximately 11,500 tourists per year from locations around the world (UWA, 2016, personal communication). During these one-hour excursions, tourists are arranged into small groups of six to visit a chimpanzee subgroup from a community that contains over 120 individuals. Although most visitors are likely conservation minded (Kanagavel et al., 2014; Juvan et al, 2014), we hypothesized that visitors might engage in behaviors that inadvertently expose the chimpanzees to reverse zoonotic pathogens. Furthermore, non-tourists engaged in support activities (e.g. guides and other personnel) also frequent the forested habitats where chimpanzees live and could be a source of inadvertent infection. The aim of this study was to describe behaviors that might affect reverse zoonotic transmission to chimpanzees at this site, and thus to help management authorities mitigate such risks in the future.

## 5.2. Methods

*Study Site*

Kibale National Park, Uganda is a mid-altitude forested park approximately 795 $km^2$ (Chapman et al., 2005). We collected data on visitors during tourist excursions to the Kanyanchu Chimpanzee community. The community's home range is about 50 $km^2$ and the tourists frequently encounter chimpanzees in fruit trees (Gruetzmacher, 2018; Chapman et al., 2018; UWA, 2018). This community is frequently visited by tourists, though other chimpanzee communities in the park are the subjects of long-term research at the Ngogo and Kanyawara stations (Muller et al., 2007; Goldberg et al., 2008; Scully et al., 2018; Gruetzmacher et al., 2018; Negrey et al., 2019).

*Behavioral Observations*

Data were collected from June 14th to August 12th, 2018, for a total of 101 excursions over 52 days. Excursions are led by the Uganda Wildlife Authority and conducted three times daily: 8 am (morning), 11 am (mid-morning), and 2 pm (afternoon), each lasting 2-5 hours, with one hour for viewing the chimpanzees. Our sampling effort was distributed evenly among these different viewing times.

Before excursions began, tourists presented their permits or payments and listened to a short safety briefing. This briefing includes the following information: basic park information (history, species present, etc.), rules and regulations (no eating, flash photography, littering, etc.), chimpanzee specific information (community composition, typical behaviors, habituation process, etc.), and activity information (length of activity, what to wear or carry, etc.). Tourist groups were then divided and mandated to have no more than six people per group, including their guide and any interns, students or researchers. Groups departed simultaneously, often from different trail entrances and remained in contact via radio. When chimpanzees were spotted, guides communicated through radios to ensure all tourists were able to view chimpanzees, often leading to group merges.

Data on visitors (including park guides, tourists, and interns) and the chimpanzees were collected by DG using a prescribed ethogram; as well DG added any behaviors deemed relevant. These behaviors were grouped into six categories: Self-Grooming, Bodily Functions, Eating, Safety Features and Concerns, Direct Forest Interactions, and Between Human Interactions. All occurrences of a behavior in the ethogram by any individual were recorded during the excursion. Three indicators of chimpanzee health were recorded: cough, sneezing, and diarrhea, with fecal matter consistence assessment corroborated by park guides. The following visitor group dynamics were also recorded: initial group size, group size while merged, distance while viewing both arboreal and terrestrial chimpanzees, distance while viewing arboreal chimpanzees, distance while viewing terrestrial chimpanzees, and time spent viewing chimpanzees. Merging occurred when two excursion groups met in the forest and remained together for longer than five minutes.

**5.3. Data Analysis**

Human behaviors and chimpanzee health indicators were analyzed using frequency tables. Human behaviors were totaled and divided by the number of excursions (N=101). In the case of chimpanzee health indicators, counts were grouped by month and divided by the number of excursions per month (June = 26, July = 52, August = 23).

The following parameters were analyzed using one-sample t-tests: initial group size, group size while merged, distance while viewing both arboreal and terrestrial chimpanzees (A&T), distance while viewing arboreal chimpanzees (A), distance while viewing terrestrial chimpanzees (T), and time spent viewing chimpanzees. Hypothetical values, noted as Recommended values, are based on IUCN (International Union for the Conservation of Nature) and UWA (Uganda Wildlife Authority) regulations.

**5.4. Results**

*Human Behavior*

There were a total of 15 park guides, 10 interns, and 434 tourists (N=459) that visited the chimpanzees during the study period. “Self-Grooming” occurred during 100.0% of excursions, followed by “Direct Forest Interactions” (99.0%), and “Bodily Functions” (94.1%) (Table 1; Figures 1 & 2). Within a category, touching large tree trunks or branches was the most frequent human behavior, followed by face-to-hand contact.

**Table 1.** Total instances of recorded human behaviors during 101 visitor excursions, grouped by six behavioral categories.

| Category | # Instances | # Excursions | % Excursions |
|---|---|---|---|
| **Self-Grooming** | **12654** | **101** | **100.0** |
| Aerosol sunscreen/bug spray | 2 | 10 | 9.9 |
| Biting/Cleaning fingernails | 32 | 32 | 31.7 |
| Chapstick/Lipstick | 2 | 2 | 2.0 |
| Eye drops | 1 | 1 | 1.0 |
| Face to hand contact | 12584 | 94 | 94.1 |
| Face wipes | 1 | 1 | 1.0 |
| Hand sanitizer | 5 | 5 | 5.0 |
| Q-tip (twig) | 1 | 1 | 1.0 |
| Toothpick (twig) | 25 | 25 | 24.8 |
| Wash hands | 1 | 1 | 1.0 |
| **Bodily Functions** | **965** | **95** | **94.1** |
| Bleeding | 4 | 4 | 4.0 |
| Coughing | 733 | 89 | 88.1 |
| Defecating | 1 | 1 | 1.0 |
| Sneezing | 154 | 66 | 65.4 |
| Spitting | 16 | 13 | 12.9 |
| Urinating | 57 | 37 | 36.6 |
| **Eating** | **42** | **17** | **16.8** |
| Breakfast Foods (bread, eggs, millet) | 5 | 7 | 6.9 |
| Leaves | 1 | 1 | 1.0 |
| Lunch items (sandwiches, potatoes, protein bars) | 20 | 11 | 10.9 |
| Snack Foods (protein Bars, crackers, g-nuts, gum) | 16 | 25 | 24.8 |
| **Safety Features and Concerns** | **403** | **70** | **69.3** |
| Age/12-yr old | 1 | 1 | 1.0 |
| Approaching chimps | 30 | 21 | 20.8 |
| Dehydration | 1 | 1 | 1.0 |
| Dropped Gun | 1 | 1 | 1.0 |
| Earphones while walking | 1 | 1 | 1.0 |
| Falling | 21 | 18 | 17.8 |
| Flash camera | 21 | 21 | 20.8 |
| Gloves | 15 | 15 | 14.9 |
| Guide safety warnings | 279 | 30 | 29.7 |
| Handle feces | 1 | 1 | 1.0 |
| Ill/sick | 4 | 4 | 4.0 |
| Imitating chimp calls | 20 | 20 | 19.8 |
| Lighter | 1 | 1 | 1.0 |
| Loud music (community nearby) | 5 | 5 | 5.0 |
| Phone call | 1 | 1 | 1.0 |
| Tourist lost | 1 | 1 | 1.0 |
| **Direct Forest Interactions** | **23669** | **100** | **99.0** |
| Drop forest artifact after touching (fruit, leaves, feathers, snake skins) | 83 | 60 | 59.4 |
| Kiss tree | 1 | 1 | 1.0 |
| Littering | 7 | 6 | 5.9 |
| Removed fruit | 1 | 1 | 1.0 |
| Sitting on forest floor | 561 | 79 | 78.2 |
| Touching (large tree trunks or branches) | 23014 | 98 | 97.0 |
| Walking stick | 1 | 1 | 1.0 |
| Wiping hands on leaves | 1 | 1 | 1.0 |
| **Between Human Interactions** | **170** | **54** | **53.5** |
| Hand Holding | 160 | 53 | 52.5 |
| Kissing | 10 | 7 | 6.9 |

*Group Dynamics*

The total number of groups to embark at any given time ranged from 1 to 6, for a range of 3 to 60 individuals in the forest at the same time. Mean group size while merged was significantly larger than IUCN recommendations of six people per group. Mean distance while viewing both arboreal and terrestrial chimpanzees, mean distance while viewing arboreal chimpanzees, and mean time spent viewing chimpanzees were different than the expected eight meter minimum distance and 60 minute viewing time allowance.

The mean distance between tourists and chimpanzees was significantly higher than IUCN recommendations when chimpanzees were in trees and on the ground (i.e., tourists were further than the eight meter minimum, but when chimpanzees were on the ground, the mean distance was shorter than the eight meter minimum). On average, groups were merged 40% of the total excursion time (55.5 ± 32.0).

**Table 2.** Visitor group size, distance to chimpanzees and time spent visiting chimpanzees in Kibale National Park, Uganda.

| | Group Characteristic | Recommended Value: | Observed Value: | Std. Dev. | t | df | *p* | α |
|---|---|---|---|---|---|---|---|---|
| 1 | Mean initial group size (# of persons) | 6.0 | 6.0 | 1.2 | 0.3 | 100.0 | 0.80 | 0.05 |
| 2 | Mean group size while merged (# of persons) | 6.0 | 18.3 | 5.2 | 23.1 | 93.0 | p<0.001 | 0.05 |
| 3 | Mean distance while viewing (m) | 8.0 | 13.7 | 6.3 | 8.8 | 96.0 | p<0.001 | 0.05 |
| 4 | Mean distance while viewing arboreal chimpanzees (m) | 8.0 | 21.3 | 9.5 | 13.0 | 86.0 | p<0.001 | 0.05 |
| 5 | Mean distance while viewing terrestrial chimpanzees (m) | 8.0 | 6.7 | 2.3 | 5.2 | 87.0 | p<0.001 | 0.05 |
| 6 | Mean time spent viewing (min) | 60.0 | 79.1 | 22.0 | 8.7 | 100.0 | p<0.001 | 0.05 |

*Chimpanzee Clinical Signs*

Counts of chimpanzee clinical signs (respiratory cough, sneezing, diarrhea) are reported per month. Signs were not evenly distributed throughout all excursions, so grouping by month better demonstrates chimpanzee population health over the three-month period. There was a high frequency of respiratory cough during June (3.04 ± 4.28) but it was lower in July (0.61 ± 1.55) and August (0.13 ± 0.63). Chimpanzees also sneezed multiple times in July (0.33 ± 0.77) as compared to June (0.04 ± 0.20) and August (0.04 ± 1.21), but diarrhea was rare during all months (Table 3).

**Table 3.** Frequency of three chimpanzee health indicators per month: respiratory cough, sneezing, and diarrhea.

| Month | Respiratory Cough | | Sneeze | | Diarrhea | | Total Excursions |
|---|---|---|---|---|---|---|---|
| | (#) | (%) | (#) | (%) | (#) | (%) | (#) |
| June | 17 | 65.4 | 1 | 3.8 | 1 | 3.8 | 26 |
| July | 11 | 21.2 | 11 | 21.2 | 1 | 1.9 | 52 |
| Aug | 1 | 4.3 | 1 | 4.3 | 0 | 0 | 23 |

*Photographs*

**Figure 1.** Fruits and vegetation touched by multiple humans during tracking excursions before being dropped onto the forest floor.


**Figure 2.** Visitors during chimpanzee excursions. A. A large group of tourists observe a singular chimpanzee. B. A large group of tourists observe multiple arboreal chimpanzees. C. A singular tourist observes a juvenile terrestrial chimpanzee from a close, crouched position.

### 5.5. Discussion

Great ape ecotourism is a “double edged sword” in that it simultaneously provides economic incentives for conserving apes while also putting them at risk for reverse zoonotic infection. Our study quantified potential modes of transmission from humans to chimps that could inform future disease risk prevention strategies. “Self-Grooming” and “Direct Forest Interactions” were the two most common behavioral categories recorded for tourists. Additionally, we documented 150% larger group sizes while merged and

125% longer chimpanzee viewing times than recommended. Although the majority of human behaviors recorded pose little risk of transmission (guide warning, dropped gun, headphones while walking, etc.) each singular instance of face-to-hand contact or touching forest artifacts could potentially lead to transmission, even if the subject is not clinically ill (Homsy, 1999; Taylor et al., 2001; Blumstein et al., 2017; Edemekong & Huang, 2019). Using twigs as Q-tips or toothpicks, spitting, bleeding, coughing, sneezing, urinating, defecating, walking shirtless, eating and depositing food scraps on the forest floor, and handling or tasting forest artifacts also pose serious risks and must be monitored to limit the spread of disease (Homsy, 1999; Taylor et al., 2001; Williamson & Macfie, 2010; Gilardi et al., 2015; Blumstein et al., 2017; Edemekong & Huang, 2019). This study presents the array of human behaviors present, allowing conservation interventions to be tailored around the few most harmful.

Studies have primarily focused on airborne pathogens and direct contact as modes of zoonotic disease transmission (O'Leary & Fa, 1993; Keet et al., 2000; Gessain, 2013; Salem et al., 2019; Manuel et al., 2019; Brown et al., 2019). However, seasonal effects and infection through fomite and environmental interaction may be potential factors (Kraav et al., 2018; Petrono, 2018; Oma et al., 2018; Krug et al., 2011). Petrono (2018) suggested human coronavirus (OC43) found in wild chimpanzees in Cote d'Ivore may have been inadvertently introduced in the forest via asymptomatic shedding, meaning the presence of virus in the absence of clinical signs or symptoms. Via shedding or contact with the environment, pathogens can be transferred and remain on the forest floor, leaves, etc. well after the subject walks away leaving chimpanzees and other organisms open to infection (Brinkworth & Pechenkina, 2013; Edemekong &

Huang, 2019). These findings reveal that the modes of reverse zoonotic transmission from people to apes may be more varied than previously thought.

For Kanyanchu, we recommend increasing activity fees to mitigate the cost of providing visitors with walking sticks, face masks, and hand sanitizer, to lessen the threat of face-to-hand contact and touching the forest (Williamson & Macfie, 2010; Ruson, 2014; Gilardi et al., 2015; Hanes, 2011, 2018; Grobusch et al., 2018). To track chimpanzees for one hour in Kibale National Park, foreign non-residents pay $150 (UWA, 2018). To track gorillas in Bwindi National Park, foreign tourists pay $600 (UWA, 2018). That is a 25% difference and tourism at both sites has only continued to increase (Simplicious Gessa, personal communication). This price increase could help to maintain or even increase income while also deterring some from participating in the activity, lowering the number or tourists observing chimpanzees on a daily basis. To continue offering chimpanzee tracking as an inclusive activity, promotions and discounts could be used at certain, limited, times of the year. To compensate for the lower number of guides needed for tracking excursions, more efforts could be made towards community conservation and law enforcement. Despite having caring and knowledgeable staff, sites such as Kanyanchu can only do so much with the funding they have. The goal is therefore to increase prices and use that money to enhance the safety of the park with a focus on limiting the risk of zoonotic disease transmission, otherwise in the future, a catastrophic outbreak could diminish tourism.

We recognize the limitations of this study being that observations were only recorded at one ecotourism site over a short period of time, and no samples were collected to document actual instances of disease transmission. However, based on the current literature and the array of behaviors seen, it is possible that fomite and environmental contact could lead to reverse zoonotic disease transmission and seriously threaten the lives of these already endangered animals.

Although these interventions are suggested based on the findings at Kanyanchu, this research suggests the need for similar evaluative strategies at ecotourism sites across the globe. We suggest that IUCN regulations take into consideration the difficulties ecotourism sites face from lack of funding and management and provide resources that train managers to evaluate and counter their site's individual challenges and concerns. No two ecotourism sites are the same, so instead of adhering to umbrella guidelines, continuously evaluating and tailoring conservation strategies on the ground is a more direct way to mitigate disease risk and maintain ecosystem health worldwide.

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