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COMMENTARY

Human Impacts, Disease Risk, and Population Dynamics in the Chimpanzees of Gombe National Park, Tanzania

ANNE E. PUSEY[1,2*], MICHAEL L. WILSON[1–3], AND D. ANTHONY COLLINS[4]
[1]*Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, Minnesota*
[2]*The Jane Goodall Institute's Center for Primate Studies, University of Minnesota, St. Paul, Minnesota*
[3]*Department of Anthropology, University of Minnesota, St. Paul, Minnesota*
[4]*The Jane Goodall Institute, Gombe Stream Research Centre, Tanzania*

The introduction of new diseases can have devastating effects. For example, Eurasian diseases such as smallpox and measles killed millions of Native Americans following the Spanish conquest [Crosby, 1972; Diamond, 1997; McNeill, 1977]. A grave concern facing primatologists is that by habituating primates to human presence for close observation, we have created frequent and varied opportunities to expose primates to new disease agents. However, it is clear that disease is not the only factor in the complex relationship between humans and nonhuman primates. The recent article by Köndgen et al. [2008] has a twofold message: human presence in the form of research and tourism protects chimpanzees from poaching and human diseases from the same researchers and tourists endanger them. The question is how to proceed with these activities in a way that maximizes survival of the primates being studied, visited, and managed by people. A first step is to examine the situation in several different study sites to review the commonalities and differences. Are the benefits and costs of human activities the same at all sites or do they vary with the particulars of the sites? Here we report on the experience from Gombe, the longest chimpanzee field study.

The chimpanzee population of Gombe in Tanzania lives at the easternmost edge of the entire chimpanzee range where the mountainous habitat supports a mosaic of riverine forest and woodland, giving way to drier miombo woodland in the east. Particularly fertile areas of evergreen forest occur in the valleys sandwiched between the eastern edge of Lake Tanganyika and the rift escarpment that rises from the lakeshore (770 m.a.s.l.) to a ridge of peaks in the east (1,300–1,600 m.a.s.l.), which parallel the lake. In the 1940s, the British government established the small Gombe Stream Game Reserve in a remnant of forest and woodland located 15–30 km north of Kigoma town to protect the chimpanzees and their habitat from deforestation by the rapidly growing human population [Moreau, 1945]. The reserve formed the basis for the current Gombe National Park, a narrow strip of land between Lake Tanganyika and the rift escarpment of 35 km^2, approximately 14 km long and 2–3.5 km wide.

BENEFITS OF RESEARCH

Jane Goodall began her research on the Gombe chimpanzees in 1960. The international attention brought to these chimpanzees led President Julius Nyerere to declare the reserve a National Park in 1968. There is no doubt that the added protection afforded by National Park status has had a highly beneficial impact on the chimpanzee population. Analysis of aerial photos and satellite images shows that the woody vegetation and forest cover have increased inside the park over the last 40 years, probably as a result of regeneration and plant succession in areas that were previously farmed, and protection from fire [Pintea, 2007]. In contrast, the areas outside the park, including forest reserves, have suffered almost total deforestation and conversation to farmland. Long-term records of diet, ranging, and grouping behavior of the chimpanzees indicate that the diet quality inside the park has increased over this time [Pintea, 2007]. In addition, although snares are found at the edges of the park, these are removed by park rangers and only one chimpanzee is known to have been injured by a snare, compared with up to 25% of the chimpanzees in habituated populations in the Kibale forest, the Budongo forest, and the Taï forest that are crippled by snares [Boesch & Boesch-Achermann, 2000; Reynolds, 2005; Wrangham & Mugume, 2000]. Given the rapid human population growth in this area of Tanzania over the past few decades, it is highly

*Correspondence to: Anne Pusey, Department of Ecology, Evolution and Behavior, 1987 Upper Buford Circle St. Paul, MN 55108. E-mail: pusey001@umn.edu

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unlikely that the Gombe chimpanzees would still be there were it not for the attention brought to them as a result of Jane Goodall's work and their consequent protection by Tanzania National Parks.

In addition to stimulating added protection for these chimpanzees, research at Gombe has also provided other benefits to chimpanzee conservation. By revealing the fascinating and complex world of chimpanzees, Goodall's early work excited not just the scientific community, but also a global audience. Individual Gombe chimpanzees have captured the hearts of thousands and serve as ambassadors for chimpanzee conservation, at least partly because of the close physical and emotional bond Goodall developed with them that she described and illustrated in her popular articles, books and films [e.g., Goodall, 1963, 1965, 1967, 1971, 1990, 1999, 2003]. Using the fame derived from her Gombe studies, Jane Goodall has become an effective advocate for the conservation and welfare of chimpanzees and general stewardship of the earth [e.g., Goodall & Bekoff, 2002; www.janegoodall.org; Goodall & Berman, 1999]. Long-term research at Gombe and other sites has provided a general understanding of chimpanzee social structure and habitat requirements, essential for effective conservation [Pusey et al., 2007].

POSSIBLE ADVERSE EFFECTS OF PEOPLE INSIDE THE PARK

Köndgen et al. [2008] document major declines in the numbers of several chimpanzee communities in the Taï forest following habituation for research. They provide compelling evidence that some of these deaths are from epidemics of human origin, although substantial mortality also resulted from Ebola and anthrax epidemics, which do not come directly from human sources. Moreover, they report that ''about half of the long-term chimpanzee research populations have shown major declines.'' This raises the questions of whether similar population declines have occurred at Gombe, and the extent to which disease has played a role in population dynamics. The Gombe National Park currently contains three communities, Mitumba in the north, Kasekela in the middle, and Kalande in the south. Jane Goodall began studying the Kasekela community in 1960. By 1966 when habituation was complete, the Kasekela community contained about 60 individuals. Over the last 40 years it has fluctuated between 38 and 62 individuals, and it contained 62 individuals in January 2008 (Fig. 1b). The size of the Mitumba community was unknown until the 1980s, at which time it was thought to contain at least 30 individuals, and probably more. The high quality of the forest in the park's northern valleys, and the persistence of the Mganza Forest Reserve north of the park until the 1990s, suggest that this area could have supported as many as 50 chimpanzees. Habituation of the Mitumba community began in the mid-1980s and was more or less complete by the mid-1990s. In 1988 and 1990, habituators observed parties with 30–32 individuals present, suggesting that the total community size was even larger (D. Mjungu, unpublished data). Since 1996, the number of individuals known to be present in Mitumba has fluctuated between 25 and 20 (Fig. 1a). The Kalande community also appeared to be strong in the 1980s with estimates ranging as high as 50–80 individuals [Greengrass, 2000a], though given the poorer habitat quality in that portion of the park we think it is unlikely that the Kalande community included many more than 40 chimpanzees. This community has never been habituated but it has been monitored since 1999 [Greengrass, 2000a]. Data from nest transects, molecular markers, and observations of known individuals indicate that the community contained at least 30 individuals in 1998 [Wilson et al., in preparation]. By January 2008, Kalande contained 11 known individuals, some of whom were sometimes seen associating with Kasekela chimpanzees and were thus likely in the process of transferring (Fig. 1c).

Major causes of the decline in numbers of the two outer communities are thought to be habitat loss and killing by people. Unlike the Kasekela community, whose range has been completely within the boundaries of the protected area since the beginning of the study, anecdotal reports suggest that both the Mitumba and Kalande communities ranged extensively outside the park in earlier decades [Pusey et al., 2007]. Both communities still do so, but to a lesser extent. Habitat loss in those portions of their former range outside the park has accelerated greatly in the last 20 years [Pintea, 2007; Pusey et al., 2007]. In addition to losing habitat, circumstantial evidence suggests that people have killed several individuals from each community outside the park in the last decade, and that at least one Kalande chimpanzee was killed inside the park by poachers [Greengrass, 2000a,b; Pusey et al., 2007]. Following the drastic decline of the Kalande community in the last decade, three mothers with dependent offspring visited the Kasekela community from Kalande and one transferred permanently. Although nulliparous females commonly emigrate to a new community at adolescence [Pusey, 1979], mothers with dependent offspring rarely transfer, presumably because of high risk of infanticide [Wilson & Wrangham, 2003]. Other cases in which parous females have transferred with offspring followed known [Nishida et al., 1985] or suspected [Emery Thompson et al., 2006] declines in the mothers' home communities, including the death of all adult males [Nishida et al., 1985]. These transfers further reduced the Kalande numbers and augmented the Kasekela community.

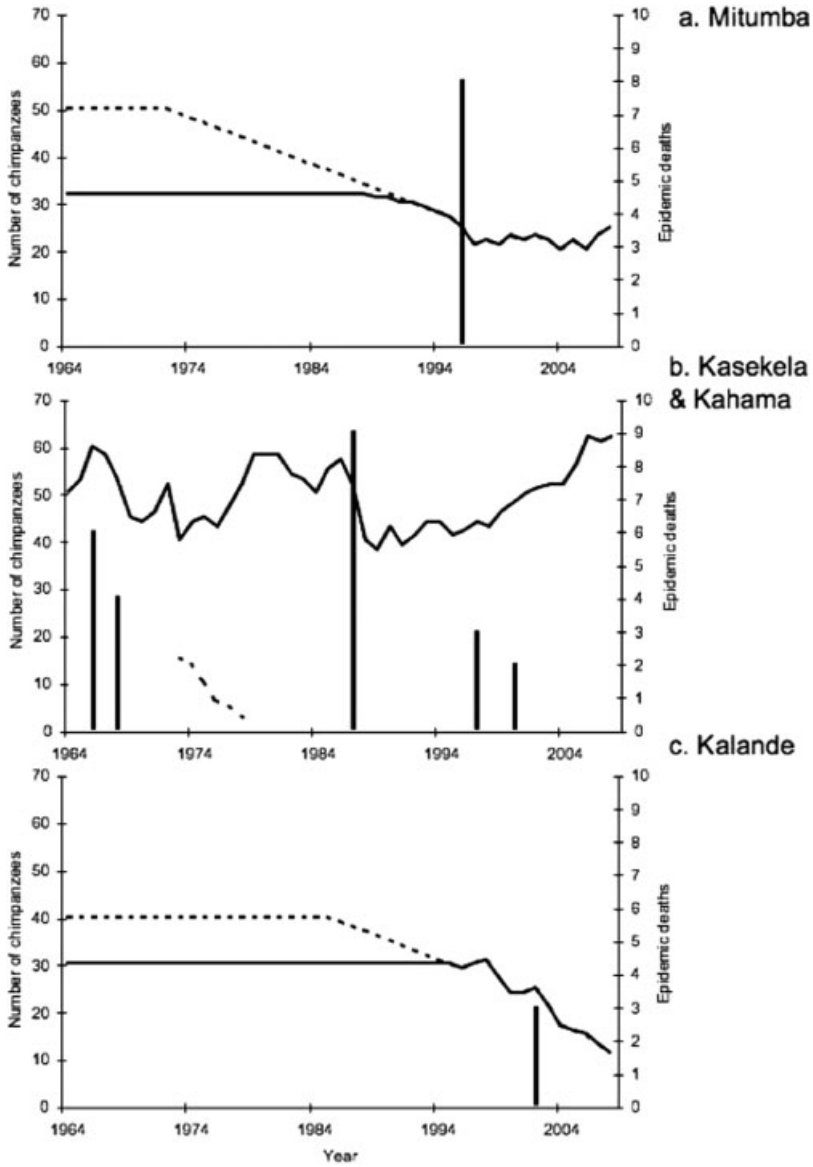

Fig. 1. Population dynamics and epidemic disease deaths for the four chimpanzee communities studied in Gombe National Park, Tanzania, 1964–2008. Lines indicate the number of chimpanzees known or estimated to exist in each community on January 1st of each year for the following communities: (**a**) minimum (solid line) and maximum (dotted line) estimates for Mitumba; (**b**) actual size for Kasekela (solid line) and Kahama (dotted line); and (**c**) minimum (solid line) and maximum (dotted line) estimates for Kalande. Estimates for Mitumba and Kalande before regular monitoring are based on few observations and are thus highly uncertain. Vertical columns indicate the number of known deaths from epidemic disease for each community [following Lonsdorf et al., 2006; Williams et al., 2008].

The impact of disease on community dynamics has been most completely studied in the Kasekela community. Although disease is the major cause of death in this community as at other sites [Boesch & Boesch-Achermann, 2000; Nishida et al., 2003], it has not wrought the devastating population decline documented at Taï. A recent analysis of causes of death in the Kasekela community over the last 40 years found disease to account for 58% of 86 deaths of known cause [Williams et al., 2008]. A total of 50% of the deaths from disease occurred during epidemics. Major epidemics included a polio-like disease in 1966 (six deaths), mange in 1997 (three deaths), and respiratory epidemics in 1968 (four deaths), 1987 (nine deaths), and 2000 (two deaths) (Fig. 1b). The symptoms of the respiratory diseases were similar to those described by Köndgen et al. [2008]. Despite sporadic epidemics throughout the study period the Kasekela community has not declined in number. Moreover, a preliminary matrix analysis of population growth based on the vital rates observed in the Kasekela community over the last 40 years shows that the growth rate is approximately zero rather than negative (J. H. Jones et al., unpublished

data). This result is very different from that derived from the composite life table compiled from data from five long-term study sites including Gombe's Kasekela community presented by Hill et al. [2001], which showed a strongly negative growth rate, presumably weighted by higher mortality at the other sites. Thus, the Kasekela community so far seems to have fared better than study communities in Taï and Mahale. And while the Kanyawara community in Kibale has declined, the more recently habituated Ngogo community in Kibale remains the largest studied chimpanzee community, with approximately 150 members [Mitani, 2006].

Three reasons that the Kasekela community may have maintained its size in the face of periodic epidemic diseases should be considered. First, efforts have always been made at Gombe to dose sick chimpanzees when this has been feasible [Goodall, 1986]. Chimpanzees were given polio vaccine in bananas in 1966 during the ''po1io'' epidemic, badly affected chimpanzees were given single doses of Ivermectin in eggs and bananas during the mange epidemic, and some sick individuals were given antibiotics in bananas during the 2000 respiratory epidemic. However, the effectiveness of such dosing is doubtful partly because very sick individuals (or immigrants that have not experienced provisioning) often do not eat baited food and also because it is difficult to find the same individual every day to complete the course of antibiotics. Second, data from remote sensing showing increased forest in the park, as well as evidence from long-term data that certain fruits have increased in the diet and the average party size has increased over the last 40 years, suggest that food availability for chimpanzees inside the park has increased [Pintea, 2007]. Thus, any decreases in population growth because of disease might have been balanced by increased population growth because of an increased food supply. Investigation of changes in food availability at other sites would be interesting. Third, increases in the Kasekela community in the last decade have occurred partly because of a larger number of immigrant females than in previous decades perhaps because of the collapse of the Kalande community. However, until 2003 all these were nulliparous females that would probably have transferred anyway, and only the increase because of one parous female and her offspring that transferred in the last 5 years can definitely be ascribed to the collapse of the Kalande community.

Our knowledge of the incidence and impact of disease in the other two communities, Mitumba and Kalande, is much less complete. One serious respiratory epidemic has occurred in the Mitumba community since habituation began in the mid 1980s. This occurred in 1996, 6 years after the start of intensive provisioning with bananas, and killed eight individuals or 32% of the community [cf. 11 reported in error by Wallis & Lee, 1999] (Fig. 1a). Efforts were made to dose chimpanzees at the feeding station using septrin in bananas. One male who failed to complete the antibiotic series seemed to improve but later died 2 months after the others. The only direct evidence we have of disease in the unhabituated Kalande community occurred in 2002, when several individuals were observed with symptoms of respiratory disease and at least three died (Fig. 1c). This occurred at the same time that a respiratory epidemic sickened most of the Kasekela community individuals but killed none. The possibility exists that a transferring female or other inter-community contact transmitted this infection from Kasekela to Kalande.

Köndgen et al. [2008] suggest that close proximity of humans to chimpanzees as a result of habituation increased the incidence of epidemics. At Gombe there has been continuous close proximity between chimpanzees and several different populations of humans since the early years of the study. Even before the study began, there was a history of sporadic interaction between chimpanzees and people. Reports from the 1800s describe well-established villages along the shore of the lake and in the hills [Burton, 1860; Stanley, 1895]. It is likely that historically most chimpanzee communities in the area had human settlements within their range. Thomas [1961] describes interactions between chimpanzees and people in the 1950s as the chimpanzees raided crops such as oil palms and bananas, and sometimes attacked human infants. However, the research process greatly increased the incidence of close proximity with people. Two years into her study, Goodall started provisioning the chimpanzees with bananas at her camp in the Kakombe valley, and as she gained their trust she sometimes groomed and played with six of the individuals in the first few years [Goodall, 1986].

To reduce such contacts, and to obtain better control over which chimpanzees got bananas, Goodall moved the provisioning to an artificial provisioning station in the center of the Kasekela community's range, and provided bananas daily from 1964 to 1967 [Goodall, 1986; Wrangham, 1974]. Although the bananas were dispensed from electronically operated boxes, and deliberate contact with the chimpanzees was forbidden, researchers spent hours every day in close proximity to the chimpanzees at the feeding station as they lost their fear of humans. Provisioning was reduced in 1968 so that each chimpanzee only received a few bananas every 7–10 days. This reduction in provisioning greatly reduced but did not eliminate chimpanzee attendance at the feeding area, where chimpanzees continued to come into close proximity with human observers. In the Mitumba community efforts to habituate the chimpanzees by provisioning with bananas began in the mid-1980s and became daily

in 1990. In this case bananas were sometimes handed directly to the chimpanzees [Wallis & Lee, 1999]. Following the respiratory epidemic in 1996, bananas were washed in disinfectant before provisioning in both communities. All provisioning was halted in 2000.

Researchers started following the Kasekela chimpanzees throughout their range in 1968, and they have been followed daily, all day, since the early 1970s. The Mitumba chimpanzees have been followed daily since the late 1990s. A rule has always been in place to keep at a distance of at least 5 m while following the chimpanzees, but this distance is often reduced by the chimpanzees themselves when they walk close to an observer who is not immediately able to move away because of the very thick vegetation. Since 2000, the minimum distance was increased to 7.5 m for researchers who had been through quarantine and 10 m for tourists. However, in practice, enforcing these regulations is difficult, especially in the thick vegetation, and especially when tourists seek to get at least as close as the researchers are to chimpanzees.

The number of expatriate researchers from the US and Europe increased from three in 1964 to more than 20 between 1972 and 1975. During this 4-year period, new pairs of undergraduates from the US arrived every 3 months and stayed for 6 months, and these were accompanied into the forest by Tanzanian field assistants from local villages. In 1975, following the kidnapping and subsequent release of four students by rebels from Zaire, expatriate researchers except for Jane Goodall were banned from the park for safety reasons. By this time the staff of Tanzanian field assistants had been trained to collect data at the feeding area and follow the chimpanzees. Since then, this team of field assistants has maintained the daily data collection, with shifts of 2–6 research personnel spending time with the chimpanzees in each community each day. Since the late 1980s the number of expatriate researchers has increased again to a maximum of about six at any one time. Tourism at Gombe began in the late 1970s, with annual numbers of foreign tourists increasing from about 300 in 1983 to 700 in 1987 and 950 in 2007 (TANAPA unpublished data). These tourists have always visited the Kasekela community for chimpanzee viewing and often get as close to the chimpanzees as the researchers do. Over the course of the busiest days at Gombe, some Kasekela chimpanzees may be visited by as many as 30 people.

Throughout the study researchers, and sometimes their families, have resided in the Kakombe valley at the center of the Kasekela community range in simple buildings with pit latrines and trash pits. These were initially sited around the lower valley, but from 1975 were re-sited along the lakeshore, outside the forest. National Park staff were first quartered in valleys outside the Kasekela community range, but in 1975 they were stationed at Kakombe. The majority moved to headquarters built at the base of the Mitumba valley in the early 1990s. From 1979, tourists were accommodated at various campsites and in a hostel in the Kakombe village. A luxury tented camp was later built at Mitumba in 2003. Other tourists come on day trips from Kigoma. Ever since the chimpanzees became used to people they have often foraged and traveled near human dwellings. They frequently stole cardboard boxes, clothes, or other articles and sucked and chewed them.

Another source of human contact has been the presence of fishermen. When the Gombe Stream Game Reserve was established in the 1940s, permanent residents and farmers were excluded from the reserve, but fishermen were allowed to continue to reside in temporary settlements along the lake shore to fish with lights and dry their catch of freshwater sardines on the beaches during the less moonlit part of the month. A series of public footpaths ran east through the reserve, enabling fishermen to travel to and from permanent villages on the other side of the rift escarpment, and their wives to bring them supplies. The number of fishermen residing on the park's beaches and the periods of the year during which they were present increased, especially in the early 1980s when they began to use seine nets that required larger teams and could be employed even on moonlit nights. It is estimated that over 1,000 fishermen were in the park at times by the mid-1980s [Goodall, 1990]. When seine-net fishing was banned by the Tanzanian government in 1998, all the fishermen ceased to live in the park. From the late 1960s, chimpanzees of the Kasekela community visited the fishermen's camps and huts when they were unoccupied and licked ash from the hearths, chewed on sleeping mats and other items, and even scavenged remains of fruit and sugar-cane from their open trash pits.

Clearly the Kasekela chimpanzees have been exposed to close human presence for the last 45 years at rates that are probably higher and more extensive than those at Taï. The Mitumba community has also had frequent close exposure to people since the 1980s, but the Kalande community has not. Yet it is the Kalande community that has shown the worst population decline. Although none of the epidemics at Gombe have been definitively traced to humans, it is likely that the ''polio'' epidemic and at least some of the respiratory epidemics have been of human origin. The mites causing the mange epidemic were closer to animal than human mites [Walton et al., 2004], but could have originated from domestic animals. The sporadic distribution of deaths from epidemics despite continuous interaction with humans raises the possibility that the Kasekela chimpanzees may have developed some immunity to at least some common human diseases. Studies of antibodies would be informative in this regard. One

possibility is that the Kasekela chimpanzees, having gained immunity to common human diseases, have served as vectors, transferring disease to naïve chimpanzees of other communities. Although adjacent communities have hostile relations and usually avoid each other, close contact during intercommunity aggression occasionally occurs, and adolescent females transfer between communities, sometimes traveling to and fro several times before settling. The Mitumba chimpanzees were not yet habituated during the 1987 epidemic in Kasekela, but observers did report one individual with symptoms of respiratory disease. The Kasekela chimpanzees did not suffer an epidemic during the 1996 epidemic in Mitumba. However, the coincidence of deaths in Kalande and a nonlethal epidemic in Kasekela in 2002 raises the possibility that the disease was transferred from the relatively immune Kasekela community to the Kalande community where individuals naïve to the disease became sicker. It is possible that this could have happened in previous years as well, but there is no evidence.

Disease represents a serious risk to chimpanzees. It is the most common cause of death, and years with epidemic diseases have seen substantial population declines for both the Kasekela and the Mitumba communities. We strongly recommend that all reasonable precautions be taken to avoid disease transmission between humans and chimpanzees. Indeed, since 2002, health rules have been in place at Gombe including immunizations and quarantine periods for researchers, regular health screenings of employees, checks on health of all visitors to the chimpanzees, and strict rules for conduct in the forest [Collins, 2003]. Recognizing that disease is the greatest source of mortality for chimpanzees at Gombe, Lonsdorf and colleagues [Lonsdorf et al., 2006; Lukasik, 2002; Travis et al., 2008] have led a health-monitoring program to better understand rates and causes of disease in this population, and to better guide preventative measures and interventions. Nonetheless, it is striking that the Kasekela community has been able to maintain its population size over nearly 50 years of observation. With the benefit of hindsight, we can identify adverse human impacts, but nonetheless the Kasekela chimpanzees have proven to be relatively resilient. Moreover, the Kasekela community, at the center of the park, has enjoyed the benefits of strong park protection and improving habitat quality from fire suppression. The Mitumba community, at the north of the park, has also generally enjoyed strong park protection and improving habitat within the park, but has suffered from loss of habitat outside the park, and has probably incurred losses from killings of chimpanzees outside the park. The Kalande community, in the south of the park, has suffered from habitat loss outside the park, killings of chimpanzees outside the park, and during some time periods an apparently lower level of protection within the park (and/or higher poaching pressure). We do not know the extent of deaths from disease in Kalande, and it is possible that this community might have suffered to a greater extent from human diseases to which the other communities in the park had already acquired immunity. However, the opportunity for such disease transfer has existed for decades, whereas the timing of the decline (late 1990s to early 2000s) appears closely linked to the conversion of adjacent areas outside the park from woodland to agriculture in the 1990s.

In summary, disease from human sources clearly represents an important threat to chimpanzee populations. Appropriate measures should be undertaken to minimize the risk of inter-species disease transmission. However, it is also clear that populations of chimpanzees—similar to other primates—face many grave dangers, including hunting and habitat loss. Returning to the metaphor of the Spanish conquest of the Americas, Native American populations declined from multiple factors, including warfare, slavery, and famine, in addition to disease [Livi-Bacci, 2006]. Populations protected from slavery and warfare, as in the missions of Paraguay, not only survived but increased in number, despite recurring outbreaks of smallpox and other diseases [Livi-Bacci, 2006]. Likewise, when we consider the threats facing primates in the wild, we see that disease is but one of many sources of mortality, and one from which primates can recover, provided that they are protected from habitat loss and hunting.

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REFERENCES

Boesch C, Boesch-Achermann H. 2000. The chimpanzees of the Taï forest: behavioral ecology and evolution. Oxford: Oxford University Press.

Burton RF. 1860. The lake regions of Central Africa (reprint). New York: Dover Publications.

Collins DA. 2003. Health guidelines for visiting researchers in Gombe National Park to minimize risk of disease transmission among primates (updated 8/01/03). Pan Africa News 10:1–3.

Crosby AJ. 1972. The Columbian exchange: biological and cultural consequences of 1492. Westport, CT: Greenwood Press.

Diamond J. 1997. Guns, germs, and steel: the fates of human societies. New York: W.W. Norton & Co.

Emery Thompson M, Newton-Fisher NE, Reynolds V. 2006. Probable community transfer of parous adult female chimpanzees in the Budongo Forest, Uganda. Int J Primatol 27:1601–1617.

Goodall J. 1963. My life among wild chimpanzees. Natl Geogr Mag 124:272–308.

Goodall J. 1965. New discoveries among Africa's chimpanzees. Natl Geogr Mag 128:802–831.

Goodall J. 1967. My friends the wild chimpanzees. Washington, DC: National Geographic Society.

Goodall J. 1971. In the shadow of man. London: Collins.

Goodall J. 1986. The chimpanzees of Gombe: patterns of behavior. Cambridge, MA: Belknap Press.

Goodall J. 1990. Through a window: my thirty years with the chimpanzees of Gombe. Boston: Houghton Mifflin Company.

Goodall J. 2003. Fifi fights back. Natl Geogr Mag April 2003: 76–89.

Goodall J, Berman P. 1999. Reason for hope. New York: Warner, Books, Inc.

Goodall J, Bekoff M. 2002. The ten trusts: what we must do to care for the animals we love. San Francisco: Harper.

Greengrass E. 2000a. The sudden decline of a community of chimpanzees at Gombe National Park. Pan Africa News 7:5–7.

Greengrass E. 2000b. The sudden decline of a community of chimpanzees at Gombe National Park: a supplement. Pan Africa News 7:25–26.

Hill K, Boesch C, Goodall J, Pusey AE, Williams JM, Wrangham RW. 2001. Mortality rates among wild-living chimpanzees. J Hum Evol 40:437–450.

Köndgen S, Kühl H, N'Goran PK, Walsh PD, Schenk S, Ernst N, Biek R, Formenty P, Mätz-Rensing K, Schweiger B, Junglen S, Ellerbrok H, Nitsche A, Briese T, Lipkin WI, Pauli G, Boesch C, Leendertz FH. 2008. Pandemic human viruses cause decline of endangered great apes. Curr Biol 18:260–264.

Livi-Bacci M. 2006. The depopulation of Hispanic America after the conquest. Popul Dev Rev 32:199–232.

Lonsdorf EV, Travis D, Pusey AE, Goodall J. 2006. Using retrospective health data from the Gombe chimpanzee study to inform future monitoring efforts. Am J Primatol 68:897–908.

Lukasik M. 2002. Establishing a long term veterinary project for free-ranging chimpanzees in western Tanzania. Pan Africa News 9:13–17.

McNeill WH. 1977. Plagues and peoples. New York, NY: Anchor.

Mitani JC. 2006. Demographic influences on the behavior of chimpanzees. Primates 47:6–13.

Moreau RE. 1945. The distribution of the chimpanzee in Tanganyika Territory. Tanganyika Notes Records 14:52–55.

Nishida T, Hiraiwa-Hasegawa M, Hasegawa T, Takahata Y. 1985. Group extinction and female transfer in wild chimpanzees in the Mahale National Park. Tanzania Z Tierpsychol 67:284–301.

Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K. 2003. Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. Am J Primatol 59:99–121.

Pintea L. 2007. Applying satellite imagery and GIS for chimpanzee habitat analysis and conservation. Ph.D. Thesis, University of Minnesota, St. Paul, MN.

Pusey AE. 1979. Intercommunity transfer of chimpanzees in Gombe National Park. In: Hamburg DA, McCown ER, editors. The great apes. Menlo Park, CA: Benjamin/Cummings. p 464–479.

Pusey AE, Pintea L, Wilson ML, Kamenya S, Goodall J. 2007. The contribution of long-term research at Gombe National Park to chimpanzee conservation. Conservation Biol 21:623–634.

Reynolds V. 2005. The chimpanzees of the Budongo Forest. Oxford: Oxford University Press.

Stanley HM. 1895. How I found Livingstone in Central Africa (reprint). Mineola, NY: Dover Publications.

Thomas DK. 1961. The Gombe Stream game reserve. Tanganyika Notes Records 56:35–39.

Travis DA, Lonsdorf EV, Mlengeya T, Raphael J. 2008. A science-based approach to managing disease risks for ape conservation. Am J Primatol 70:745–750.

Wallis J, Lee DR. 1999. Primate conservation: the prevention of disease transmission. Int J Primatol 20:803–826.

Walton SF, Dougall A, Pizzutto S, Holt D, Taplin D, Arlian LG, Morgan M, Currie BJ, Kemp DJ. 2004. Genetic epidemiology of *Sarcoptes scabiei* (Acari: Sarcoptidae) in northern Australia. Int J Parasitol 34:839–849.

Williams JM, Lonsdorf EV, Wilson ML, Schumacher-Stankey J, Goodall J, Pusey AE. 2008. Causes of death in the Kasekela chimpanzees of Gombe. Am J Primatol 70:766–777.

Wilson ML, Wrangham RW. 2003. Intergroup relations in chimpanzees. In: Durham WH, editor. Annual Review of Anthropology. Polo Alto, CA: Annual Reviews Inc., p 363–392.

Wrangham RW. 1974. Artificial feeding of chimpanzees and baboons in their natural habitat. Anim Behav 22:83–93.

Wrangham RW, Mugume S. 2000. Snare removal program in Kibale National Park: a preliminary report. Pan Africa News 7:18–20.