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Chimpanzee Conservation: What We Know, What We Do Not Know, and Ways Forward

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Introduction

Biodiversity is being lost at an accelerating rate, with current extinction rates approximately 1,000 times higher than background rates observed in the fossil record (Pimm et al. 2014). Recent estimates suggest that 11,000–58,000 species are lost annually and that extant vertebrate species have declined in abundance by approximately 25% since 1970 (Dirzo et al. 2014). Humans are clearly responsible for this accelerating loss of biodiversity by causing habitat conversion, climate change, the spread of exotic species, and wildlife overexploitation (Dirzo et al. 2014; Laurance et al. 2012; Ripple et al. 2015). This has led to almost 50% of the world's primate species being at risk of extinction (Estrada 2013; Estrada et al. 2017; Mittermeier et al. 2009), and 14.5% being critically endangered (IUCN Redlist database 2020).

The endangerment of chimpanzees (*Pan troglodytes*) is particularly important because of their iconic status and phylogenetic closeness to humans. It is estimated that chimpanzee populations have experienced a significant reduction in the past 20 to 30 years and the overall population reduction over three generations is estimated to exceed 50% (Walsh et al. 2003), hence qualifying this taxon for endangered status. It is officially estimated that only half a million chimpanzees exist in the wild, with 65,000 in West Africa, 9,000 in Nigeria and Cameroon, 140,000 in Central Africa, and 256,000 in the Democratic Republic of Congo above the Congo River and in East Africa (Humle et al. 2016). However, other estimates suggest much lower numbers (Oates 1996; Sop et al. 2015) and the level of endangerment and the nature of the threats differ among regions and across subspecies (Kühl et al. 2017).

Chimpanzees occur at low densities and they are very difficult to habituate and follow for scientific observations due to their fission-fusion social system and large home range (Bertolani and Boesch 2008; Boesch and

Boesch-Achermann 2000). As a result, to evaluate conservation threats to chimpanzees it is useful to take a comparative approach and contrast them to other diurnal primates that inhabit the same forest. These other primates are easier to study and census, thus there is much more data on their response to adverse conditions people create. Therefore, in our evaluation of chimpanzee conservation, we will draw on a number of examples of how monkeys respond to threats that similarly affect chimpanzees. However, it is important to acknowledge that chimpanzees represent something special. They can be considered to fill important roles as umbrella, flagship, or phylogenetically important species (Hartel et al., chapter 26 this volume; Wrangham et al. 2008). As such, many would argue that they deserve special attention. Directing conservation efforts to chimpanzees can make great advances at fostering public awareness and raising funding for conservation. Chimpanzee conservation efforts must include a myriad of activities, including protecting their habitat, decreasing bushmeat hunting, and improving park-people interactions, thus conserving chimpanzees conserves their habitats and the plants and animals therein.

The objective of our review is to document current threats to chimpanzee populations in such a way as to illustrate what the scientific and conservation communities know and what they do not know. In doing so, we hope to illustrate the way forward for both communities. There are likely thousands of publications, government documents, reports from NGOs, and theses published every few years on chimpanzee abundance and distribution. Therefore, this is not meant to be an exhaustive review, but rather we focus on major issues. We concentrate our evaluation on the populations in East Africa, particularly Uganda, as this is an area we work in and know well; however, we make comparisons with threats facing other chimpanzee populations, as well as other African primate species, to put chimpanzees' conservation concerns in context.

Deforestation

Threats to chimpanzees come in many forms, but likely one of the most significant is habitat loss (Morgan et al., chapter 27 this volume). Between 2000 and 2012, it is estimated that 2.3 million km2 of forest was lost globally, and in the tropics rates of loss increased by 2,101 km^2 per year (Hansen et al. 2013). To put this in perspective, the global annual loss is approximately the size of Mexico (1.96 million km^2). The loss is greatest in South America and Africa. However, estimates of deforestation vary greatly. For example, a recent study estimates a 62% acceleration in deforestation in the humid tropics between

TABLE 25.1. Landsat estimates of forest area (106 ha) in 1990, 2000, and 2010 for different countries in Tropical Africa, with data from Kim, Sexton, and Townshend (2015)

Country	*1990*	*2000*	*2010*
Cameroon	20.32	20.21	19.88
Congo	23.88	23.66	23.43
Democratic Republic of Congo	153.23	152.2	147.93
Equatorial Guinea	2.59	2.56	2.54
Gabon	23.38	22.92	22.99
Liberia	7.46	7.27	7.23
Madagascar	8.93	8.55	7.58
Sierra Leone	3.76	3.70	3.53
Total	**243.55**	**241.07**	**235.11**

1990 and 2000 (Kim, Sexton, and Townshend 2015) that dramatically contradicts the 25% reduction reported by the Food and Agriculture Organization of the United Nations (FAO 2010). This is regrettable as conservation biologists do not really know the magnitude of the problem they are dealing with and thus have a difficult time estimating the impact on chimpanzee populations. Furthermore, in such circumstances policy makers have the option of selecting the lower deforestation estimates when they establish policy if that suits their needs. By one estimate Africa shows the largest accelerating rate of loss (table 25.1) (Kim, Sexton, and Townshend 2015), which is alarming when one is considering chimpanzee conservation. The largest loss, and the largest increasing rate of forest loss, is in the Democratic Republic of Congo. This loss will be accentuated by the discovery of oil reserves in the Virunga National Park and the desire to exploit this resource (Gouby 2015). The oil industry opens up roads that are used to extract bushmeat and the oil workers hunt to feed themselves (Wilkie 2000). Per-country deforestation rates are a function both of the pace of logging and conversion to agriculture and of how much forest remains. For example, in Uganda, closed-canopy tropical forest once covered 20% of the country's land area, but deforestation reduced this to just 3% by 1990 (Howard et al. 2000), thus in terms of km2 there is not much left to lose. However, Uganda still lost 18% of its remaining forest between 1990 and 2000 (Howard et al. 2000) and the most recent estimate suggests that the annual rate of loss of tropical high forest is 7% (Pomeroy and Tushabe 2004). Very soon, Uganda will have little or no forests left that could support chimpanzee outside of the three forested National Parks (Chapman, Lawes, and Eeley 2006; Chapman et al. 2013). Deforestation rates in Uganda, however, pale in comparison to other African countries that harbor chimpanzees. The worlds' highest deforestation range, according to the FAO (2010), is Nigeria and it is estimated that between 2000 and 2005, Nigeria lost 55.7% of its primary forest, while the rural poor saw few advances in the quality of life. One should not simply think of these values as a strict loss in forest; rather, they also represent a fragmentation and the genetic isolation of populations. From that perspective, deforestation has resulted in the fragmentation of 58% of the subtropical forests and 46% of tropical forests (Chapman et al. 2007; Estrada et al. 2017; Haddad et al. 2015).

These statistics represent the general loss of forest; however, chimpanzees are a very flexible genus, being found in woodland and riverine forests to dense closed high-canopy forests (Hockings et al. 2015; see also Pruetz, Bogart, and Lindshield, chapter 17 this volume). Thus, the overall decline in suitable habitat, not just forest, would be a more accurate metric. A recent study predicted the distribution of suitable environmental conditions for chimpanzees in the 1990s and 2000s and demonstrated that the area of suitable habitat declined by 207,827 km^2, from 2,015,480 to 1,807,653 km^2 (i.e., an area approximately the size of the US state of Kansas or just larger than the country of Senegal) (Junker et al. 2012). This represents a 10.3% decline in a decade, and the authors of the study conclude that this represents a dramatic decline in suitable environmental conditions and call for an immediate increase in conservation efforts. In addition to this, the number of suitable areas did not decline significantly, suggesting that the size of suitable areas has shrunk. This raises the serious question of whether existing populations are large enough to maintain viable populations in the long term. A second study predicted that by 2030 only 10% of the current African great ape habitat will remain (Nelleman and Newton 2002).

In general, chimpanzee habitat loss corresponds with an increase in agriculture in tropical countries, which globally expanded by 48,000 km^2 per year between 1999 and 2008 (Phalan et al. 2013). One estimate suggests that approximately 1 billion ha of additional agricultural land, primarily in developing countries, will need to be converted to agriculture by 2050 to meet the demands of the growing human population—an area larger than Canada (Laurance, Sayer, and Cassman 2014). Ultimately, these changes are driven by increased human population size and consumption rates (Crist, Mora, and Engelman 2017). The UN Population Division estimates that the world's population is expected to rise from 7 billion in 2011 to 9 billion in 2050. Making the situation more dire for chimpanzees is the fact that, in primate range countries in Africa, human population density in 1950 was 8 people/km^2, while in 2010 it had increased to 35 people/km^2 (Estrada 2013) and in some protected parks harboring chimpanzees, human population density neighboring the park exceeds 400 people/km^2 (Hartter et al. 2015; MacKenzie and Hartter 2013). Also, as prosperity in tropical countries increases, there is a tendency for people to want to eat higher on the food chain (e.g., cattle), which demands greater land conversion.

Chimpanzees are a charismatic species that can be a rallying point for conservation effects and conserving their populations is the morally correct thing to do. As a result, it is an urgent imperative that we attempt to reverse a number of these trends and given that many populations may be approaching the point where they are no longer viable, the time for action is now.

Bushmeat

The bushmeat trade is a large commercial and local industry that is decimating many animal populations, particularly in West and Central Africa (Fa, Peres, and Meeuwig 2002; Walsh et al. 2003). The need to understand the bushmeat trade is partially created by the fact that a large proportion of the remaining chimpanzees are not in protected areas—approximately 45–81% of West African chimpanzees are not in parks or reserves (Kormos et al. 2003). However, hunting is frequently a serious problem in protected areas as well (Refisch and Koné 2005). For example, in Budongo Forest Reserve, Uganda, 21% of chimpanzees suffer from limb injuries caused by hunting snares (Byrne and Stokes 2002) and in Kibale National Park, Uganda, 31% of identified chimpanzees over the age of two exhibited limb disability (Cibot et al. 2016; Hartel et al., chapter 26 this volume). This is not an issue localized to Uganda: Quiatt, Reynolds, and Stokes (2002) documented that 32 of 422 chimpanzees (7.6%) in 10 different communities across Africa had limb disabilities likely resulting from snares.

There are a number of single-case market studies (Covey and McGraw 2014; Martin 1983), and hunting and the sale of ape meat have been reported from Nigeria (McFarland 1994), Central African Republic (Goldsmith 1995), Democratic Republic of Congo (Basabose, Mbake, and Yamagiva 1995), Gabon (Harcourt 1980), and Equatorial Guinea (Fa et al. 1995). This is not just a local trade; it is an international trade. Chaber et al. (2010) report that 273 tonnes of bushmeat are confiscated annually at the Charles de Gaulle airport in Paris, France. Assuming that the weight of the average cow is 625 kg (weight of an average Canadian cow, but an average Ankole cow in Uganda weighs 485 kg), this would mean that the equivalent of 440 cows were confiscated. This does not include the bushmeat that was not detected, the importation into other airports in France or worldwide, or the bushmeat that may come in through other routes, such as via shipping or over land. However, despite this sort of information on the extent of general bushmeat hunting, there is little large-scale evidence or quantification of bushmeat hunting impacts on populations of chimpanzees, and most studies simply examine the quantity of all bushmeat and do not distinguish between animal species (reviewed by Taylor et al. 2015).

While not informing chimpanzee endangerment, some of these bushmeat studies reveal some alarming statistics. For example, it has been estimated that four million metric tons of bushmeat were extracted each year from the Congo basin alone (equivalent to approximately 4,500,000 cows, Fa and Brown 2009). The rate of extraction was estimated to be increasing by 90,000 tonnes each year in 2002 and the rate of increase may have gone up (Fa, Peres, and Meeuwig 2002). In a study considering bushmeat on a species-by-species basics, Kano and Asato (1994) estimated that in the Mataba River region of northeastern Republic of Congo, 0.02 chimpanzees were killed annually per km^2. This represents an annual offtake of 5–7%, which, given chimpanzee's slow life history strategy, is unsustainable. Two country-wide surveys have been done in Côte d'Ivoire over a decade apart (1989–1990 and 2007) in national parks and classified forests, and on Mount Kope. These surveys documented a 90% decline in chimpanzee nest encounter rates over 17 years and attributed the decline to the 50% increase in the human population (Campbell et al. 2008). Distressingly, this study illustrates that even the national parks that are intended to be refuges for chimpanzees and other animals are not functioning as safe havens, and species in parks can still be driven to extinction through hunting (see also Laurance et al. 2012; McGraw 2005; Oates et al. 2000). Such trade from parks is very common in many regions. In a global analysis of 60 parks, Laurance et al. (2012) documented that researchers consider only approximately half of all reserves to have been effective over the last 20–30 years, while the remainder of the reserves are experiencing an alarming erosion of biodiversity, which includes the loss of primate species. This phenomenon is poignantly illustrated by a park-wide survey in Taï National Park, Côte d'Ivoire: regardless of primate species, density was 100 times higher near the protected research station and tourism site than in the remainder of the park (N'Goran et al. 2012). Similarly, in Moukalaba Doudou National Park, Gabon, surveys demonstrated that ape nest density (distinguishing chimpanzee and gorilla nests is not possible) was threes time lower at the park borders near human population centers, as compared to the park interior (Kuehl et al. 2009).

Associated with the bushmeat trade is the lucrative illegal trade of chimpanzees to discreditable zoos (often privately owned or in developing countries) and private owners. A baby chimpanzee can fetch $12,500 US, and often more (Shukman and Piranty 2017), and China has been singled out as the main destination for many of these illegally trafficked apes (Stiles et al. 2013). But the cost to the population is much larger than the one animal that makes it to these markets—hunters will typically shoot as many adults as possible to prevent adults from interfering with the capture of the baby and to get animals for bushmeat. An inquiry by the British Broadcasting Corporation estimated that for every infant captured, 10 adults would be killed (Shukman and Piranty 2017).

Disease

A further threat to chimpanzees is from disease, particularly Ebola (Walsh et al. 2007). However, surprisingly little is known about Ebola's impact on chimpanzees at the population level. This is partially due to the fact that researchers working on behavior and ecology have not been closely connected with researchers in the medical and veterinary fields, though this is changing rapidly (Goldberg, Paige, and Chapman 2012; Goldberg et al. 2008; Leendertz et al. 2006b; Rouquet et al. 2005). It is also due to the fact that chimpanzee populations typically inhabit remote forest regions, where road access is limited at best and researchers often lack access to those regions and are thereby unable to document disease outbreaks. Thus, Ebola outbreaks are often inferred from either low chimpanzee densities or declines in densities (Huijbregts et al. 2003; Walsh et al. 2003). The most dramatic case where the decline was estimated occurred in the Lossi Sanctuary in northwest Republic of Congo, where the chimpanzee population declined by more than 80% (Bermejo et al. 2006; Leroy et al. 2004). Another well-documented case involved a habituated chimpanzee community in Taï National Park, Côte d'Ivoire, where 11 of 43 (26%) members of one group disappeared in 1994, and where Ebola was confirmed as the cause (Boesch 2008; Formenty et al. 1999).

Diseases other than Ebola may also threaten chimpanzee populations (Knott and Harwell, chapter 1 this volume). Anthrax has been documented to have killed at least six individuals in Taï National Park (Leendertz et al. 2004) and at least three individuals in Cameroon (Leendertz et al. 2006a). Respiratory diseases have also caused deaths of chimpanzees at Kibale National Park, Uganda (Scully et al. 2018), Taï National Park (Kondgen et al. 2008), and Gombe National Park, Tanzania (Pusey, Wilson, and Collins 2008) and some of these infections are believed to have been transmitted to chimpanzees from people and vise versa. For example, molecular and epidemiologic analyses demonstrated that the outbreak of a respiratory disease in the chimpanzees of

Kibale National Park in 2013, which killed an infant chimpanzee, was consistent with the common cold in humans (Scully et al. 2018). However, to date, peaks in respiratory cases in local clinics have not been shown to correspond to peaks in similar symptoms in chimpanzees (Chapman and Melissa Emery Thompson, unpublished data).

There is a detailed record of the causes of deaths of chimpanzees at Gombe over 40 years and analyses indicate that disease accounted for 58% of the 86 deaths where the cause of death was known (Lonsdorf et al. 2018; Pusey, Wilson, and Collins 2008; Williams et al. 2008). Furthermore, major epidemics accounted for 50% of these disease-related deaths, attributed to a polio-like disease, mange, and respiratory diseases (Pusey, Wilson, and Collins 2008).

What seems clear to us is that disease, particularly Ebola and Anthrax, can play a major role influencing the size of chimpanzee populations. However, we know relatively little about its overall impact at the population level. This calls for closer collaboration between ecologists and veterinary scientists (Leendertz et al. 2006b) and large-scale monitoring schemes (Leendertz et al. 2006b; Leroy et al. 2004)—unfortunately there does not seem to be the political will to pay for such monitoring. These actions are definitely needed if we are to be able to make informed conservation plans for chimpanzees and decrease the risk of transmission of Ebola to the human population. The link between human health and conservation warrants further investigation as this may prove to be a win-win situation (Kirumira et al. 2019).

Climate Change

Thus far, deforestation and habitat loss seem to be the major threats to chimpanzees; however, another potential threat to chimpanzee populations comes from global climate change. Admittedly this risk is one that is very difficult to evaluate, but here we present data with which we can speculate on the potential outcomes of this global phenomenon. The Intergovernmental Panel on Climate Change (IPCC) estimates that the earth warmed by 0.85°C (0.65 to 1.06°C) between 1880 to 2012 (IPCC 2014) and temperature is projected to increase by 1.5°C by 2100 (IPCC 2014). Given where primates occur, estimates suggest that they will experience 10% greater warming than this global average, and some primate species will experience a 50% greater temperature increase for every 1°C of global warming (Graham, Matthews, and Turner 2016). Primates will also face changes in rainfall. This is because rising temperature alters global patterns of circulation, which affects rainfall patterns; however, changes will not occur uniformly around the globe (Graham, Matthews, and Turner 2016). Precipitation changes will likely be quite varied across the areas occupied by primates (i.e., from >7.5% increases per °C of global warming to >7.5% decreases) (Graham, Matthews, and Turner 2016). Furthermore, there will be "climate change hotspots" and if these areas contain endangered species, the consequences could be very severe and even result in extinctions. Projections vary considerably; however, considering moderate greenhouse gas emission estimates, it is estimated that 75% of all tropical forests present in 2000 will experience temperatures that are higher than the temperatures that presently support closed canopy forest by 2100 (Wright, Muller-Landau, and Schipper 2009).

For Africa, climate change projections are that the rainforest regions will become 3 to 4°C hotter over the next century under the most likely emission scenarios (Malhi et al. 2013; Zelazowski et al. 2011). This will lead to the retreat of forest in some areas, to be replaced by woodland or savannah. With regard to how rainfall patterns will be altered in Africa with climate change, the picture is less clear. It seems likely that East African forests will become wetter. Climate models for West Africa and the Congo Basin produce conflicting results; some suggest more rain, while others suggest less (Zelazowski et al. 2011). However, as recently as 3,000 years ago, there was a substantial retreat of both of these forest types (Oslisly et al. 2013), thus a climate-change induced forest retreat is certainly a possibility (Malhi et al. 2013).

The distribution of suitable chimpanzee habitat has been modeled for Cameroon and Nigeria under three different climate change scenarios for the years 2020, 2050, and 2080 (Clee et al. 2015). The availability of suitable habitat in northwest Cameroon and Eastern Nigeria is predicted to remain largely unchanged through 2080; however, in central Cameroon, habitat is predicted to decline dramatically over the coming century. This must be taken seriously in conservation planning, because the population in Central Cameroon represents half of the population of the chimpanzee subspecies *Pan troglodytes ellioti*, and this region also experiences high levels of hunting.

Lehmann, Korstjens, and Dunbar (2010) constructed a simulation model based on chimpanzee time budgets and how they would be altered by rising temperatures and changing rainfall patterns. The authors noted that climate variability would play a particularly important role in the degree of change in ape population size and distribution. Unfortunately, few climate change models consider such variability, yet intra-annual weather variability can also strongly impact species behavior and survival. The effect of such changes on chimpanzee populations will be driven partly by such direct effects of climate change (e.g., responses to temperature, disappearing habitat), but it has become clear in recent years that the indirect effects, mediated via species interactions, could be pronounced and have very significant impacts

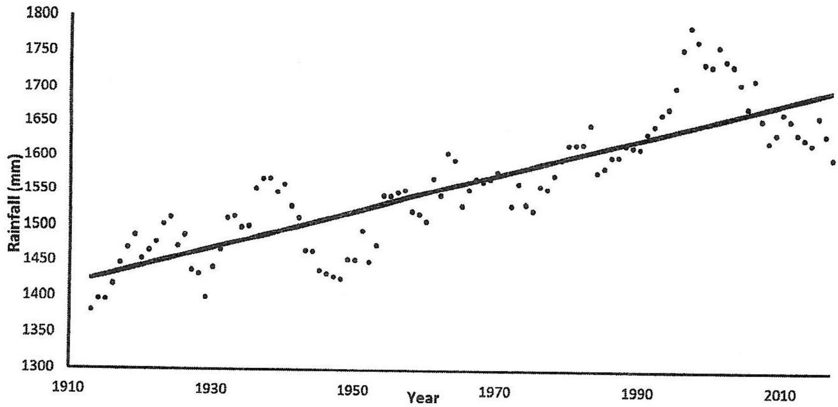

FIGURE 25.1. The 10 year running average of annual rainfall (mm) at Makerere University Biological Field Station, Kibale National Park, Uganda from 1903 to 2014.

on populations as well (Angert, LaDeau, and Ostfeld 2013). This is one area where research on other primates can inform us of what to expect chimpanzees will experience, such as our work on the red colobus (*Procolobus rufomitratus*) of Kibale National Park, Uganda.

It is relatively easy to imagine that in areas becoming hotter and drier, food trees will die and chimpanzees will die along with them or need to move. This is supported by data from Amboseli National Park, Kenya, where the average daily maximum temperature increased by 0.275°C per year between 1976 and 2000, which is an order of magnitude greater than that predicted by climate change models (Altmann, Alberts, and Roy 2002). This change corresponded to a dramatic loss of tree and shrub cover (Altmann, Alberts, and Roy 2002) and may have driven the concomitant decline in local vervet monkey populations (Struhsaker 1973, 1976). What happens in situations where the climate gets wetter is much less clear, but potentially equally negative for chimpanzees and resultant population stability. For example, Kibale National Park, Uganda, has experienced climate change well above the global average. The area receives 300 mm more rainfall/year than in 1900 and the average maximum monthly temperature has increased by 4.4 C° in the last 40 years (fig. 25.1). Corresponding with this change in climate, we have documented the cessation of fruiting of a number of plant species (Chapman et al. 2005), meaning that there is less fruit available for the frugivores, such as chimpanzees. One example of the localized effects of climate change on fruiting trees that primates rely on for food is that of *Trilepisium madagascariense* (formerly *Bosqueia phoberos*). This species has stopped fruiting at a site to the north of the park (Kanyawara) but continues to fruit at a site to the south

(Dura River), which is drier because of a natural north-south decline in rainfall associated with a decline in elevation.

In Kibale National Park there have also been changes in the quality of the leaf resources that correspond with changing temperature and precipitation. Greenhouse experiments indicate that elevated temperature, rainfall, and CO^2 to levels predicted by climate change models will impact the nutritional composition of leaves (Robinson, Ryan, and Newman 2012; Stiling and Cornelissen 2007; Zvereva and Kozlov 2006). Rothman et al. (2015) show a general increase in fiber and tannins and a decline in protein compared to data collected 15 and 30 years previously. This study examined leaves that were important in the diet of red colobus; however, this may also apply to the terrestrial herbaceous vegetation that is often considered an important fallback food for chimpanzees (Lambert 2007; Malenky and Wrangham 1994; Marshall et al. 2009; Wrangham et al. 1991). A decline in the quality of fallback foods that are eaten when more-preferred foods are not available could have serious impacts on a chimpanzee population.

The wetter conditions that East African forests will experience, and that West and Central African forests may experience (model predictions vary), are likely to create conditions where diseases become more prevalent. Connections between climate and disease are well established in the human medical literature, with specific diseases occurring during certain seasons, or erupting in association with specific unseasonable weather conditions. For example, in sub-Saharan Africa, meningococcal meningitis epidemics erupt during the hot dry season and subside soon after the onset of the rains (Patz et al. 1996). Climate change can affect disease transmission by influencing the ecology of hosts and vectors, or by causing resource shifts that stress the animal's physiology, making them more susceptible to infection (Haines and Patz 2004). For example, heavy rains are associated with outbreaks of waterborne diseases in humans. In the United States, 68% of waterborne disease outbreaks, such as *Giardia* and *Cryptosporidium* (both of which infect chimpanzees) were preceded by precipitation events above the 80th percentile (Hunter 2003). One reason that wetter conditions promote disease is that they facilitate the survival of infective stage parasitic larvae and eggs. For example, in an experimental study Larsen and Roepstorff (1999) demonstrated a reduction in the number of pig parasite eggs recovered in hot, dry months compared to wetter months. A study in Kibale National Park on black-and-white colobus (*Colobus guereza*) supports the idea that wetter conditions promote parasitism (Chapman et al. 2010). The study demonstrated that groups in wetter habitats (e.g., wet valley bottoms) had elevated gastrointestinal infections, as compared to groups in the same region that lived in drier areas (e.g., hilltops). Also, in Kibale National Park there is a north-south decline in rainfall associated with decreasing elevation and as predicted groups living in the north had elevated gastrointestinal infections compared to groups in the drier south (Chapman et al. 2010). The population effects of such changes in parasite infections remain to be evaluated.

Genetic Viability

Knowledge of patterns of chimpanzee population genetic diversity can provide pivotal insights into the evolutionary history, population structure, mating system, demographic dynamics, and population viability, which should be used to inform conservation design and recovery efforts. High-coverage genome sequencing of chimpanzees supports two distinct lineages, each comprising two genetic groups: Central/Eastern and Nigeria-Cameroon/ Western chimpanzees (Prado-Martinez et al. 2013). The Central chimpanzee shows the highest genetic diversity and largest effective population size (N_e), whereas the Western chimpanzee shows the lowest level of genetic diversity and smallest N_e among all populations (Prado-Martinez et al. 2013).

Despite the wide distribution and relatively large total population size, many of the remaining chimpanzee populations are small and dispersed. This situation is particularly severe in Senegal, Mali, the Cabinda enclave of Angola, Equatorial Guinea, and Sudan. Traditionally, the 50/500 rule has been applied to gauge the minimal viable population size of endangered species, i.e., $N_e = 50$ as the minimum population size for avoiding inbreeding depression, and $N_e = 500$ for retaining evolutionary potential. Accumulating evidence suggests that these thresholds are too low and a 100/1,000 rule might be more appropriate for the purpose of maintaining population viability in the short term, as well as the long term (Frankham, Bradshaw, and Brook 2014). It is worth noting that N_e of a wild population is often only a small fraction of the census population size, as censuses include immatures and non-breeding individuals (Frankham 1995; Palstra and Ruzzante 2008). Additionally, high variance in sex ratio and reproductive success can lead to a large further reduction of the ratio of N_e to census population size (Frankham 1995; Luikart et al. 2010). Taken together, very few extant wild chimpanzee populations fulfill the minimum population rules for conservation.

Human activity and habitat modification often increase genetic structure and limit gene flow within and among habitat areas, leading to genetic isolation and inbreeding within small populations (Knight, Chapman, and Hale 2016). High degrees of inbreeding are frequently correlated with low genetic diversity, impaired resistance to disease and environmental stress, and reduced growth rate and reproductive success, all of which hamper individual fitness and population viability (Keller and Waller 2002; Knight, Chapman, and Hale 2016). Therefore, maintaining ecological corridors is critical to ensure continued chimpanzee dispersal between habitat pockets and combat genetic erosion caused by population isolation and inbreeding (Basabose, Mbake, and Yamagiva 2015). However, genetic information of many local chimpanzee populations remains uninvestigated or sporadic at best, posing significant challenges for science-guided management. Future conservation efforts should stress genetic monitoring of chimpanzee populations to understand population dynamics and the impacts of anthropogenic disturbance and environmental variables on population demographic and genetic patterns (Schwartz, Luikart, and Waples 2007). Populations with high genetic diversity (i.e., genetic reservoirs) can potentially be of importance for genetic rescue of small, inbred populations threatened with extinction (Whiteley et al. 2015).

The genetic viability of populations should also be used by conservation managers to identify conservation priorities in situations where difficult choices have to be made, which, sadly, is often the case. If conservation managers were to follow these rules of thumb for the minimum viable population size for avoiding inbreeding depression and retaining evolutionary potential as around 1,000 breeding individuals and it was assumed that only one-third of the animals recorded in a typical census were breeding (due to the proportion of immature individuals and the sometimes small proportion of males that sire offspring), this would mean that populations of greater than 3,000 individuals should be conservation priorities. For East African chimpanzees, this would mean emphasizing conservation efforts in the Democratic Republic of Congo and potentially Uganda (table 25.2; the Central African Republic is data deficient). Let us consider Uganda in more detail (table 25.3). Of the 26 forests for which we have census data, only three (Budongo, Bugoma, and Kibale) are estimated to have 1,000 individuals, and no area has the 3,000 individuals needed to maintain the minimum population size for avoiding inbreeding depression and retaining evolutionary potential (the Bugoma Forest Reserve has experienced intense pressure recently and the previous estimates now likely overestimate what remains, C. Chapman and P. Omeja, pers. observations, May 2017). How this information is used should be debated; however, it does mean that the protection of Budongo and Kibale should be a Ugandan priority. The situation elsewhere in Africa is not unlike that in Uganda. For example, Campbell et al. (2008) report a 90% decline in the chimpanzee populations of Côte d'Ivoire between 1990 and 2007 (see also N'Goran et al. 2013).

TABLE 25.2. Estimates of eastern chimpanzee populations in each country in which they occur (adapted from Plumptre et al. 2010).

Country	*Country Size (km2)*	*Chimpanzee Population*
Burundi	27,834	450
Central African Republic	622,984	?
Democratic Republic of Congo	2,345,409	42,798
Rwanda	26,338	275
Sudan	1,886,068	?
Tanzania	947,303	2,750
Uganda	241,038	5,000
Total	**6,096,974**	**51,273**

TABLE 25.3. Estimates of the population size of chimpanzees in Uganda (NP = National Park, FR = Forest Reserve)

Area	*Population Estimate*	*Survey Year*	*Source*
Budongo NP	500–1,000	1999–2002	Plumptre, Cox, and Mugume (2003)
Bugoma FR	500–1,000	1999–2002	Plumptre , Cox, and Mugume (2003)
Bugoma–Budongo Corridor	50–100	1999–2002	Plumptre, Cox, and Mugume (2003)
Buhungiro	Extirpated	2008–2010	Koojo (2016)
Bulindi	260	2006	McLennan (2008)
Bwindi Impenetrable NP	100–300	1999–2002	Plumptre, Cox, and Mugume (2003)
Echuya FR	Extirpated	1999–2002	Plumptre, Cox, and Mugume (2003)
Ibambaro FR	Extirpated	1999–2002	Plumptre, Cox, and Mugume (2003)
Itwara FR	100–300	1999–2002	Plumptre, Cox, and Mugume (2003)
	34	2008–2010	Koojo (2016)
Kagombe FR	100–300	1999–2002	Plumptre, Cox, and Mugume (2003)
Kagorra region	<50	1999–2002	Plumptre, Cox, and Mugume (2003)
Kalinzu FR	100–300	2006	Plumptre et al. (2008)
	220	1999–2002	Plumptre, Cox, and Mugume (2003)
Kasato FR	<50	1999–2002	Plumptre, Cox, and Mugume (2003)
Kasyoha-Kitomi FR	300–500	2006	Plumptre et al. (2008c)
	370	1999–2002	Plumptre, Cox, and Mugume (2003)
Kibale NP	500–1,000	2015	Sop et al. (2015)
	1,298	1999–2002	Plumptre, Cox, and Mugume (2003)
	921	2005	Wanyama et al. (2009), Wanyama (2005)
	1,931*	No date	Plumptre and Cox (2006)
Kibego FR	<50	1999–2002	Plumptre, Cox, and Mugume (2003)
	Present	2008–2010	Koojo (2016)
Kitechura FR	Extirpated	1999–2002	Plumptre, Cox, and Mugume (2003)
Kyambura Wildlife Reserve	50–100	1999–2002	Plumptre, Cox, and Mugume (2003)
Maramagambo	100–300	1999–2002	Plumptre, Cox, and Mugume (2003)
Matiri FR	Extirpated	1999–2002	Plumptre, Cox, and Mugume (2003)
	Present	2008–2010	Koojo (2016)
Muhangi FR	<50	1999–2002	Plumptre, Cox, and Mugume (2003)

TABLE 25.3. *(continued)*

Area	*Population Estimate*	*Survey Year*	*Source*
Otzi FR	<50	1999–2002	Plumptre, Cox, and Mugume (2003)
Rwenzori Mountains NP	300–500	1999–2002	Plumptre, Cox, and Mugume (2003)
	466	2012	S. M. Koojo, unpublished data
South Bugoma	<50	1999–2002	Plumptre, Cox, and Mugume (2003)
Toro-Semliki Wildlife Reserve	50–100	2010–2011	Samson and Hunt (2012)
Wambabya FR	100–300	1999–2002	Plumptre, Cox, and Mugume (2003)

Note: Adapted from Sop et al. (2015) with additions from a variety of sources.

*Calculated.

Future Directions

There are a number of excellent studies that discuss means of reducing logging, or lessening its impact (Bicknell and Peres 2010; Morgan 2007; Morgan et al. 2017; Putz, Dykstra, and Heinrich 2000), and there are many excellent texts that discuss means to decrease the risk of disease transmission from humans to chimpanzees (Boesch 2008; Cranfield 2008; Leendertz et al. 2016; Pusey, Wilson, and Collins 2008; Rwego et al. 2008; Wallis and Lee 1999; Woodford, Butynski, and Karesh 2002). Thus, we are not going to review what has already been so well reviewed. Rather, we would like to present novel ways forward.

It should be emphasized that a large number of review studies and the recommendations from many long-term researchers point to the importance of improved and more extensive law enforcement (Struhsaker, Struhsaker, and Siex 2005; Tranquilli et al. 2012, 2014). For chimpanzees, particular attention should be paid to snare removal, which takes different search strategies than regular patrols that are searching for poachers (Muller and Wrangham 2000; Quiatt, Reynolds, and Stokes 2002). In addition, long-term research sites and tourist establishments have proven effective at reducing poaching and should be encouraged (Sandbrook and Semple 2006; Sarkar et al. accepted with revision); however, this development must be done in a fashion that minimizes the risk of disease transmission.

Education and public outreach constitute a conservation strategy that has been employed for decades. The assumption behind this is that if conservation biologists can illustrate to the community the value of a protected area, they will not exploit and harm its resources. Unfortunately, contrary to expectations, studies in Africa have demonstrated that community outreach programs designed to promote positive community attitudes through education are seldom associated with successful conservation outcomes (Struhsaker, Struhsaker, and Siex

2005). In fact, a detailed study of protected areas in Uganda found no evidence that such programs promoted positive community attitudes toward parks (Mugisha and Jacobson 2004). It is our opinion that these negative results do not mean that this approach should be abandoned, but rather we should learn from past experiences and make the approach more effective. In fact, there is a resurgence of the application of this approach (Padua 2010; Savage et al. 2010) and its careful long-term evaluation (Jacobson 2010; Kuhar et al. 2010), some of the original problems of such programs are being addressed (Kasenene and Ross 2008; Struhsaker, Struhsaker, and Siex 2005), and new refined approaches that deal with chimpanzees appear promising (Leeds et al. 2017). Since education often targets the young, the impact of such programs will be seen only after many years (Chapman, Struhsaker, and Lambert 2005; Struhsaker, Struhsaker, and Siex 2005). Also new outreach approaches should be investigated (Leeds et al. 2017).

We have initiated one such new local outreach approach involving the union of the provision of health care and conservation; namely the delivery of health care to local communities bordering Ugandan national parks through a mobile health clinic system and the establishment of a large permanent clinic (Chapman et al. 2015). The mobile health clinic is a means to reach many people; in fact, it is estimated that in its first year of operation it helped 1,000 patients a month and delivered conservation outreach information to 10,000 people a month (Kirumira et al. 2019). These examples suggest that if the goal is to conserve chimpanzees, the local communities' livelihoods must be considered so that they perceive receiving benefits from the protected areas and thus are encouraged to conserve the system and its chimpanzees. This also calls for strategic intervention in other livelihood activities for local communities so that pressure on chimpanzee habitat can be reduced.

Lastly, a number of researchers have questioned the model typically used by large governmental or non-governmental organizations to fund conservation projects (Oates 1999; Struhsaker, Struhsaker, and Siex 2005; Terborgh 1999). Typically, groups like the World Bank give large sums of money to the central government over a relatively short period of time (e.g., 5 years) and after this short period funding stops altogether. We suggest that changes should be made in funding strategies. A recent study used an evaluation of 90 "success stories" provided by conservation scientists and practitioners and explored characteristics of the projects that were "perceived" successful (Chapman et al. 2016). The conservation community viewed successful projects to most often be long-term, small spatial scale, and relatively low budget, and involving a protectionist approach alone or in combination with another approach. This suggests that extending funding over longer periods of time and investing in long-term projects would help make conservation gains.

To reduce or remove current threats across the whole range of chimpanzees will require huge efforts on a very large scale and very significant funding. It will require that international and national agencies gain the cooperation of local people, alternative sources of income and protein be found, and a great deal of effort be placed on education and outreach, with novel approaches being attempted and evaluated, increased efforts toward law enforcement, genetic monitoring of existing populations with corridors being established when possible, and protection of large areas where large populations are still found (i.e., Democratic Republic of Congo). In reality, it is unlikely that a project of such a magnitude will be initiated, but attempts must be made on whatever scale is possible.

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