Received: 4 February 2021 | Revised: 26 April 2021 | Accepted: 5 July 2021

DOI: 10.1002/evan.21920

REVIEW ARTICLE

Evolutionary Anthropology ISSUES, NEWS, AND REVIEWS WILEY

Primate conservation: Lessons learned in the last 20 years can guide future efforts

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Abstract

Twenty years ago, we published an assessment of the threats facing primates and with the passing of two decades, we re-evaluate identified threats, consider emerging pressures, identify exciting new avenues of research, and tackle how to change the system to rapidly advance primate and primate habitat conservation. Habitat destruction and hunting have increased, the danger of looming climate change is clearer, and there are emerging threats such as the sublethal effects of microplastics and pesticides. Despite these negative developments, protected areas are increasing, exciting new tools are now available, and the number of studies has grown exponentially. Many of the changes that need to occur to make rapid progress in primate conservation are in our purview to modify. We identify several dimensions indicating the time is right to make large advances; however, the question that remains is do we have the will to prevent widespread primate annihilation and extinction?

KEYWORDS
academic system change, bushmeat hunting, climate change, deforestation, microplastics

1 | INTRODUCTION

Exactly 20 years ago, we thought that the coming of the new millennium was an appropriate moment to write about threats facing primates.[1] We sought to use the article as a springboard to encourage discussions about future academic and applied research directions and hoped this would lead to positive conservation action. Now that two decades have passed, it seems fitting to re-evaluate the situation.

The picture we painted in the original article was not a new one. In 1962, François Bourlière, one of the most influential French ecologists and one of the best-known French gerontologists, wrote "Unfortunately, at the very moment when we are becoming aware of the uniqueness of the Primates..., we are also realizing how precarious is the future of the Primates and to what point competition with industrial man is threatening their survival... Can we remain unmoved at such annihilation (p. 185)?".[2] Since Bourlière made his statement the world has experienced rapid change and many of these changes have negative effects on tropical forests and the primate populations they sustain.[3,4] Overall, 75% of all approximately 512 primate species have declining populations, 65% are threatened with extinction,[4] and 14% are Critically Endangered.[5,6] It seems almost certain that Miss Waldron's red colobus (*Procolobus waldronae*) marks the first primate species to have been lost in the last century[7] and if significant actions are not implemented several species are unlikely to persist into the next century.[8,9]

The objectives of this paper, two decades after the first, are the following. First, we evaluate how the severity of the previously identified threats have changed, focusing on habitat modification and hunting. Second, we consider how issues that we previously did not view as significant have either grown in severity or our perception of their impact is no longer obscure. Here we focus on climate change and disease and consider the potential sublethal effects of microplastics and pesticides. Following this threat analysis, we assess the effectiveness of conservation strategies. Finally, we tackle the difficult issue of system change. Here we ask what upheavals need to occur in the career tracks academics pursue to bring about more rapid and effective conservation.

2 | PREVIOUSLY IDENTIFIED THREATS

2.1 | Habitat loss and degradation

Twenty years ago, we viewed that there were two leading threats to primates—habitat modification and hunting. Let us evaluate the positive and negative developments with respect to each. Habitat loss and degradation are still the major drivers of terrestrial biodiversity loss and the greatest threat to primates. Globally, ~60 million hectares of tropical primary forest were lost from 2002 to 2019, with most forest loss occurring in Brazil (24.5 Mha), Indonesia (9.5 Mha), and the Democratic Republic of the Congo (4.8 Mha).[10] To put this in perspective, an area of old-growth tropical forest larger than Madagascar was lost in 18 years. Of this, 46% occurred in the Neotropics, 30% in Southeast Asia, 21% in mainland Africa, 2% in Madagascar, and 1% in South Asia.[6] If we focus on the large scale strongholds rather than small populations, an alternative way to evaluate the situation is to consider the loss of wilderness areas, defined as large intact landscapes that are mostly free of human disturbance. It is estimated that 330 Mha of wilderness has been lost since the early 1990s, which is approximately 9.6% of the total area.[11] Nearly 50% of the remaining wilderness areas are found in the Amazon and Congo basins. It is hard to grasp the magnitude of change from such statistics, thus we obtained maps of forest cover loss from Cote d'Ivoire and the Brazilian Amazon (Figures 1 and 2).

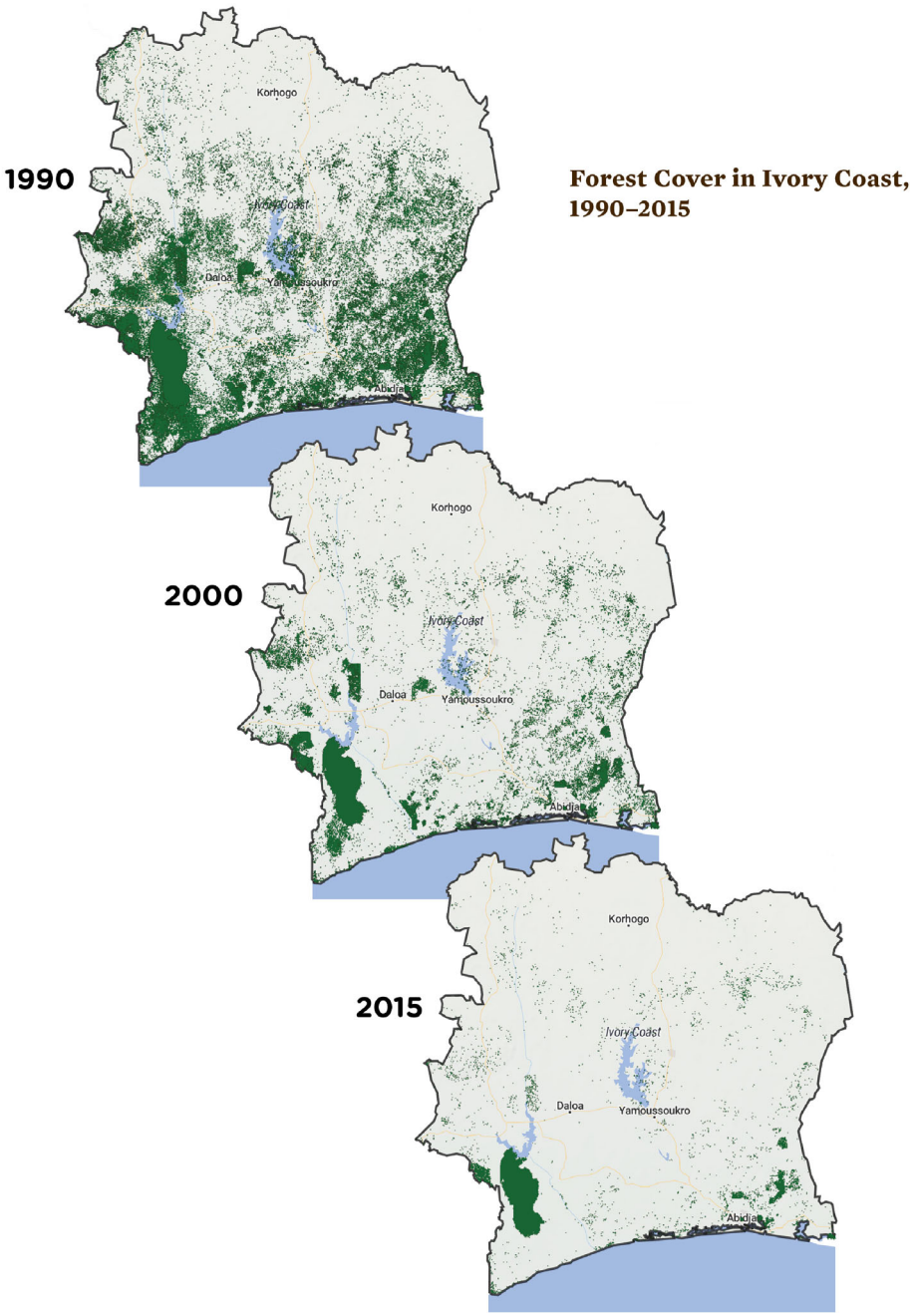

FIGURE 1 Forest cover (depicted in green) in the Ivory Coast in 1990, 2000, and 2015 (figure adapted with permission from Higonnet et al.[12]). In 2015, the remaining forest is primarily protected areas but many of the primate populations in these areas have been dramatically impacted by bushmeat hunting

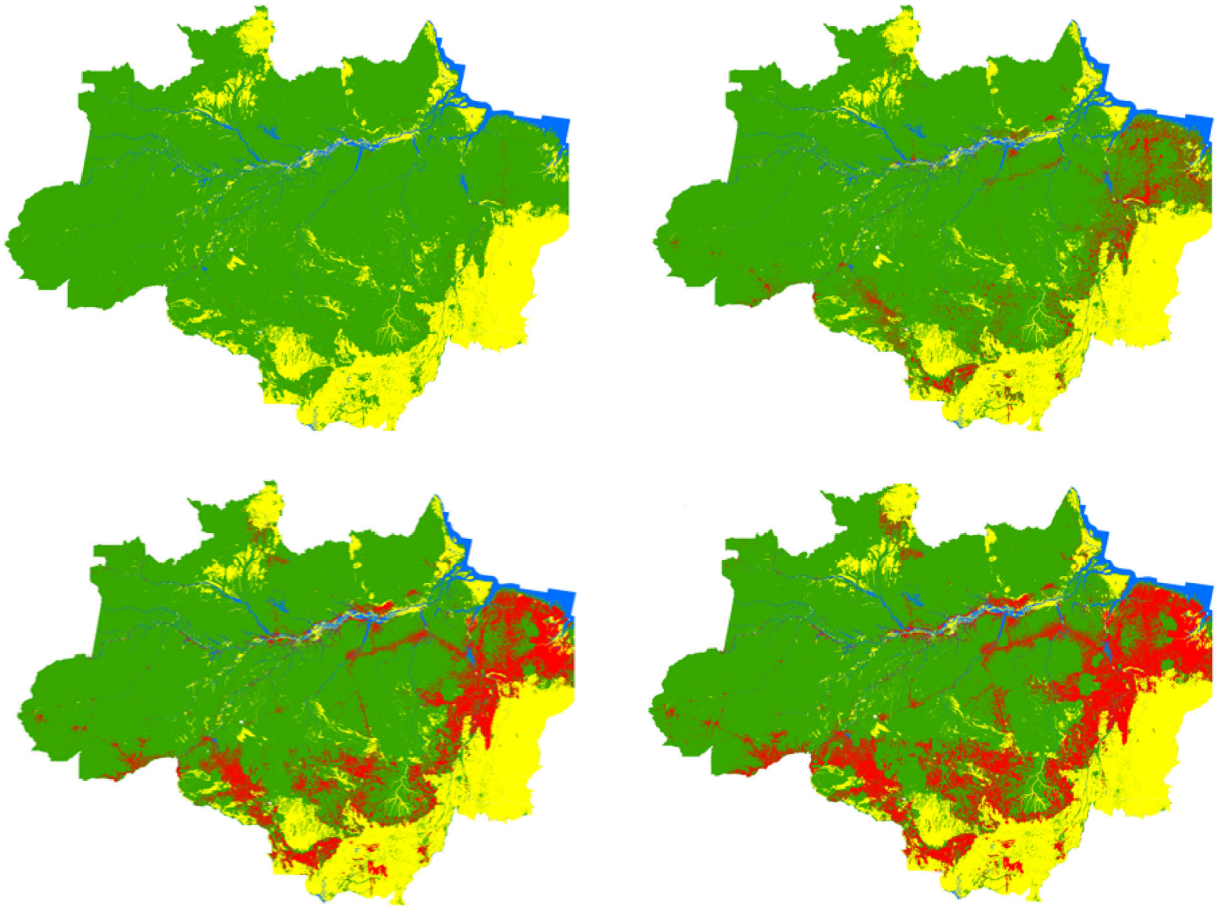

FIGURE 2 Deforestation across the Brazilian Amazon over nearly half a century. Panels left to right and top to bottom show closed-canopy forest (green areas) and previous deforestation (red areas) in 1970, 1980, 2000, and 2018. Yellow areas indicate natural non-forest land cover

This loss corresponds to a proportionate increase in croplands and cattle pastures in tropical countries, which expanded by almost half a million km^2 per year between 1999 and 2008 (about the size of Spain or Cameroon), largely at the expense of forest.[13] Estimates suggest that food production needs to increase by 1.1% each year.[14] One estimate suggests that approximately 1 billion ha of additional land—an area larger than Canada—primarily in developing countries, will need to be converted into agriculture by 2050 to meet the food demands of the growing human population.[15] The increase in human body mass and height could add 19% to this estimate.[16] In addition, per capita increases in purchase power in many tropical economies and countries like China with its large population are translating into diets at higher trophic levels, thereby inflating the average agricultural land footprint.[16] Ultimately, these changes are driven by increased human population size and consumption rates. The world's population is expected to rise from 7 billion in 2011 to ~9 billion in 2050. Further aggravating the situation for primates is the fact that the human population growth rate between 1980 and 2005 was 2.7%/yr across the three major primate biogeographic realms, amounting to a population doubling-time of 26 years.[17]

When we considered habitat degradation 20 years ago, we focused on forest loss induced by logging and timber extraction; since then, these activities have only become more important. Despite the fact that many regions no longer have significant areas of old-growth forest left to be logged (Figures 1 and 2), timber harvesting worldwide shows no signs of deceleration, thus more primate habitat is being destroyed or degraded each year.[4,17,18] Between 1960 and 2010 industrial round-wood production increased from 28 million m^3 to 155 million m^3 in Central and South America, from 23 million m^3 to 71 million m^3 in sub-Saharan Africa, and from 15 million m^3 to 30 million m^3 in Southeast Asia.[17] Harvesting two tropical trees that are about 15 m tall and 60 cm in diameter yields approximately 1 m^3 of wood, thus the 30 million m^3 harvested in South Asia comes from approximately 60 million trees. Since for every tree extracted a few other trees are killed in collateral damage, the overall tree mortality from this extraction is staggering. Furthermore, logging companies are returning to previously harvested concessions and taking out a broader range of species than they had originally, including self-standing fig trees (*Ficus* spp.), which are important foods for many primates.[19,20] Almeida-Rocha et al.[21] conducted an extensive meta-analysis based on 72 studies examining 637 comparisons between disturbed forests and adjacent pseudo-control "undisturbed" forests and documented a 30% decline in the biodiversity metrics of primates.

Since the turn of the new millennium, tropical forests have been increasingly converted into tree monocultures and this deserves special mention. The conversion to oil palm production was responsible for the loss of 30 million ha of forest between 2000 and 2011 (an area the size of the Philippines).[22] Lands under rubber production, mostly for tires, increased by 4.4 million ha between 1983 and 2012 and an additional 4.3–8.5 million ha of additional rubber plantations are required to meet projected demand by 2024.[23] Cacao production resulted in 30 million ha of land being converted between 1988 and 2008.[24] Oil palm production alone is estimated to threaten 270 million ha of tropical biodiversity hotspots.[25] These are big businesses. For example, in 2015, the global market for chocolate was approximately $100 billion and every year nearly 3 million metric tonnes of chocolate and other cocoa products are consumed globally. This is approximately the weight of half a million African savannah elephants (*Loxodonta africana*). Most of the world's chocolate is grown in primate host countries of West Africa.

2.2 | Hunting

The second major threat we considered 20 years ago was bushmeat hunting. At the time, there was limited data on the topic, but it was clear from what was known that overhunting was a major threat. Since then, our knowledge of the threat has grown substantially, as likely has the extent of hunting. Yet given extremely low fecundity, primate populations are typically overharvested even under very low offtake rates. Overharvesting is now considered by some to be the leading threat among all threatened vertebrate species, and hunting pressure has increased worldwide over the last couple of decades, in part through the use of cable snares and shotguns, despite the fact that these methods are officially banned in most tropical countries.[26,27]

The bushmeat trade is a large industry that is decimating many primate populations.[26,28] It is estimated that between 1 and 4 million tonnes of bushmeat were extracted each year from Central Africa alone[26,29] (the upper estimate equivalent to ~5.7 million bovine cattle; this would make 6.8 billion hamburgers, which are consumed in the United States in just 50 days as per capita consumption in the United States = 0.388 hamburgers per person per day). In Sarawak, Malaysia, the annual wild meat harvest is estimated to be ~23,500 tonnes,[30] while the Brazilian Amazon's annual offtake is estimated at between 67,000–164,000 tonnes.[31] These offtake levels should be viewed relative to the areas that are inaccessible to hunters. In 2003, Peres and Lake[32] used a series of long-term vertebrate censuses and calculated that only 1.2% of the Brazilian Amazon that was officially protected is reasonably inaccessible to hunters.

Such hunting rates are unsustainable and have already resulted in the eradication of populations.[27,30] For example, in the last 40 years alone, 12 large vertebrate populations have been extirpated from Vietnam.[33] Over longer timescales, human overkill was responsible for the extinction of many more species; for example the extinction of the megafauna on Madagascar[34] or the robust ateline species of Brazil.[35] Given increasing human population sizes and climate change related food insecurity, hunting rates are expected to increase.

2.3 | Fire

In our original paper we highlighted the role of fire. The destructive power of fire was fresh in our minds, because in 1997 and 1998 more than 6 million ha of forest burned in Brazil and Indonesia alone. These fires were associated with El Niño (ENSO) and Indian Ocean Dipole (IOD) climatic events. When we were writing our original paper, these were dramatic numbers and it led us to state that to advance future conservation efforts, data on the impacts of fires on primates and on forest structure and composition were critically needed. Since then, two things have happened; one positive, the other negative. On the positive side, we have gained a greater understanding of how vertebrates respond to these wildfires. For example, in the Amazon, the basal area of fruiting trees decline by 29% after a single surface fire and 62% after a second fire[36,37] and this recurrent fire leads to the extirpation of many large frugivores.[36] Similarly, in Sumatra, siamangs (*Symphlangus syndactylus*) do not use heavily burnt areas even 18 years post-fire.[38] On the negative side, the climatic events that aggravated the fires in 1997 and 1998 are increasing in frequency and intensity in association with climate change, thus they are no longer newsworthy. For example, in the fire season of 2015 Indonesia lost more than 2.6 million ha to fire, an area larger than Vermont, and these fires caused economic costs estimated to exceed US$16 billion and more than 100,000 premature deaths. Yet they did not receive the media attention of the earlier fires. The frequency of extreme positive IOD events that create the conditions for fire in Southeast Asia and Australia is predicted to increase from one event every 17.3 years during the 20th century to one every 6.3 years in the 21st century; an increase of almost three times.[39] As a result, understanding the effects of fire and discovering ways to prevent land from burning or promote forest recovery in the aftermath of fire are even more important today than it was 20 years ago.

2.4 | Habitat fragmentation

Two decades ago, we highlighted the importance of disturbed and fragmented forests for primate conservation as these landscapes were becoming so extensive. Since then, the situation has only gotten worse. Today, large areas of intact forest are rare and many primate species only inhabit small forest fragments in human-dominated landscapes.[4,40,41] In fact areas of continuous tracts of forest larger than 500 km^2 suitable for large primate populations (possibly including naturally treeless areas, with no remotely detected signs of human activity) comprise only 20% of remaining tropical forests and these forests are disappearing at a rate of 7.2% each year.[42] Only 12% of these areas are protected.[42] Predictions suggest that in the next 50 years the number of fragments will increase 33-fold and the mean size of these fragments will decline to between 0.25 and 17 ha.[43]

Unfortunately, many species are now only found in fragments. For example, a recent analysis of 22 of the 27 primate species in China suggests that 15 of these species have less than 3000 individuals, all of which living in forest fragments.[4,8,44]

We previously highlighted that in these landscapes, conservation strategies must be designed to minimize human-wildlife conflict. The academic community rose to this challenge and we have learned a great deal in the last two decades.[45,46] However, our personal experiences suggest we could have learned more. There is a strong bias in academic research only to report successes. However, we must learn from the failures or we are doomed to continuously try conservation approaches that well-intended academics think would work, but are fatally flawed. For example, around Kibale at least half a dozen efforts have been put forward to decrease crop raiding by primates through establishing bee hives along the forest edge. Each has failed in the long run, but none of these failures have been reported.

2.5 | Conservation planning

Twenty years ago, we called for conservation plans that considered and mitigated the impacts of the growing number of people on the planet and their ever-increasing consumption rate. Our call was largely ignored. Family planning and birth control is a topic that international aid agencies and many governments have simply been too afraid to discuss, never mind tackle. This inaction is manifested in high population growth rates. For example, fertility rates were projected to decline in Africa over the last two decades as they did in Latin America and Asia in the 1970s. However, the rate of decline has only been a quarter of those projected and in some African countries, the decline stalled altogether.[47] Unfortunately, this is partially attributed to the unmet need for contraception—the difference between the demand and availability is approximately 25% and this difference has not declined over the last 20 years.[47,48] The inevitable outcome of this is continued conversion of wildlands into agriculture. We encourage research and action dealing with better self-management of family demographics. One way to do this is to forge a union between the provision of health care and conservation. In Kibale we have established a clinic and mobile clinic that bring basic health care, family planning, deworming, HIV/AIDS treatment and counseling, vaccinations, and health and conservation education to remote villagers around the park.[48,49] Currently, if local community members receive treatment, they only pay for the replacement cost of the drugs they are given, and only those drugs that are not covered by the Ministry of Health. Vaccinations, deworming medicine, and anti-retroviruses for AIDS are free—hopefully we will soon be able to supply Covid vaccinations. The Mobile Health Clinic also provides educational talks focusing on issues such as family planning, sanitation, nutrition, and the value of the park to the local communities. We also let people air their grievances concerning the park so that we can seek solutions to them. The Mobile Health Clinic fosters good will, improves park-people relationships, and hopefully decreases the likelihood that local people will hunt primates and other animals.[48] Each year, we provide medical treatment to 16,000 people and outreach to about 200,000. Notably, our most popular service is family planning. Family planning is popular as women, in particular, realize the financial difficulties or raising a large family (e.g., the high costs of school) and thus want to manage family size. We encourage others to explore this model that forges a union of health care and conservation, as it has the potential to bring benefits to more people than typical ecotourism programs.

It is not only population growth rates that need to be considered, but individual consumption levels. International aid agencies and governments have not only failed to curb consumption levels, they have encouraged increased consumption as this fuels economic growth. The consequences of increased consumption have global ramifications. For example, many countries in Africa are experiencing a "land grab" by large businesses from countries that are capital rich but poor in suitable agricultural land.[50] In 2009, >50 million ha of farmland in Africa had been subject to transactions of this kind, mostly with investors from oil- or capital-rich but food-poor Middle-East or Asian countries, with the products destined for export.[51] This amount of land is roughly the size of France. These transactions can amount to a large fraction of the available agricultural land; for example, Uganda more than 14%, Mozambique more than 21%, and DRC more than 48%.[50] These acquisitions are generally made by countries attempting to secure food and feed supplies for their people and include countries in the Gulf States, China, South Korea, and India. This is partially driven by increased wealth in these countries and a concomitant growing preference for animal-based diets. The consumption of animal products requires significantly more land than vegetarian diets, and in general, wealthier people consume more food than poor people.[52] Since the food grown on these foreign-owned lands will be exported, African nations will have to put more land, often forested land, into agricultural production to meet the food needs of their growing human populations. Furthermore, when Africa experiences an environmental crisis, such as drought, the foods from these lands will be unavailable to the continent's residents. These environmental crises will increase in frequency and intensity with climate change[53] and the humanitarian crisis that will result will be extreme. It is estimated that the continent's population growth will result in an additional 36 million Africans being affected by drought-related famine by 2050.[54] When people are starving, conservation efforts will become a very low priority and people will take food, including primates, from protected areas.

3 | NEWLY RECOGNIZED THREATS

3.1 | Climate change

Ironically and sadly, 20 years ago we saw concerns over climate change primarily as an opportunity to garner interest and funding to promote forest protection and restoration. Climate change is still a great opportunity for primate conservation as forest carbon storage is high in the science and policy agenda.[55–57] However, scientists and

the public now realize that there is a myriad of cascading effects of climate change that negatively impact biodiversity.

The Earth's climate has warmed significantly as the result of human actions. The Intergovernmental Panel on Climate Change (IPCC) estimates that globally the Earth's mean surface temperature has increased by 0.87 ± 0.12°C between the 1880 and 2012 and temperature increase by the end of the 21st century is projected to exceed 1.5°C, but be less than 4°C.[53] A forecast using updated projections for human population growth estimated an increase of 3.2°C by 2100.[58] Given where primates occur, estimates suggest that they will experience 10% greater warming than this global average and some primates will experience a 50% greater temperature increase for every 1°C of global warming,[59] meaning 4.8°C increase using one projection.[58] Models predict approximately 70% of seasons in the tropics will exceed the temperature maxima of the late 20th century between 2010 and 2039.[60]

Rising temperature alters patterns of air circulation, affecting rainfall patterns.[59] Precipitation changes will be quite varied across the geographic ranges of primate.[59] In dry tropical forests where primates often rely on waterholes, such as Calakmul Biosphere Reserve in Southern Mexico, these sorts of changes will likely be too great to continue supporting forest—as annual rainfall will likely be reduced to 880 mm by 2090.[61]

Extreme climatic events that will likely become more frequent and/or more intense are of great concern (e.g., droughts, hurricanes, wildfires). A recent analysis indicates that 16% of all primate species are threatened by hurricanes and 23% are threatened by droughts.[59] In the droughts of 1997–1998, two million ha in Brazil and four million ha in Indonesia burned,[1] and threats from wildfires are only increasing. In the first seven months of 2020, more than 1.3 million ha of the Brazilian Amazon burned.[62] There will be "climate change hotspots" and if these areas contain endemic species, extinctions are very likely. For example, almost three-quarters of China's primates have populations of fewer than 3000 individuals and most of these are in the south of the country where the climate is getting significantly wetter.[8,63] Madagascar with its large number of endangered endemic species is a hotspot of climate change.[64,65]

Understanding the cascading consequences of climate change is one of the most important questions that conservation scientists must address in the next decade. Unfortunately, our abilities to predict primate responses to climate change are very poor and there remains many data gaps.[66] There are, however, estimates of what will happen to tropical forests. For example, using moderate greenhouse gas emissions scenarios, models suggest that 75% of all tropical forests remaining in 2000 will experience temperatures higher than those presently supporting closed-canopy forests by 2100.[67] For folivores, data suggests that leaves will become less nutritious. Supporting considerable evidence from greenhouse experiments, Rothman et al.[68] demonstrated an increase in fiber and a decline in protein in leaves from Kibale relative to leaves collected 15 and 30 years previously. Because many folivores select leaves with high protein to-fiber ratios, declining leaf quality could have a major impact on their abundance. Based on a predictive model between colobine biomass and the protein-to-fiber ratio of mature leaves,[69] a 31% decline in colobus monkey abundance is predicted. However, the population in Kibale has grown, possibly because of a change in the old-growth forest composition[70,71] or because the population is flexible in what it eats.

To what extent climate change will modify fruit supplies is unclear, but data is being brought to bear to answer this complex question.[72] A long-term tree phenology dataset shows that climate change contributed to severe supra-annual food shortages in West Africa, with a fruit famine induced by an 81% decline in fruiting in Lope National Park, Gabon between 1986 and 2018.[73] Two studies of trees that produce food for primates suggest climate change will impact primate numbers. A 19 years study monitoring the phenology of 20 tree species at Ngogo in Uganda found overall fruit production increased during the first half of the study, but declined thereafter.[74] The most significant predictor of monthly fruit production was temperature and production decreased with increasing temperature. The temperature of the region has increased by 2.2°C over the last 50 years.[75] A study quantified fruiting in Kibale over 185 months from 43 species and evaluated these patterns in relation to solar radiance, rainfall, and monthly temperature. It was found that solar radiance, temperature, and rainfall all showed positive effects on fruiting, with solar radiance having the strongest influence. Given regional climate change predictions, fruit availability is expected to decline as reduced solar radiance declines.

Phenological studies have focused on community level patterns. Yet, all tree species will not respond equally to climate change. Some trees are critical for primates, while others are not, and the degree of importance varies depending on what other foods are available. As a result, deciphering how specific primates will respond to climate change will be a very complex but exciting research topic in the coming decade. One group of fruiting species that will be particularly intriguing to study are figs (*Ficus* spp.), as they are well known to be important food sources for many primates. While there is little evidence that figs act as keystone species,[76,77] ripe fruits are eaten by many primates.[78] Figs are particularly vulnerable to climate change, as not only are they physiologically affected by the changing climate, but most fig species rely on a single species of fig wasp for pollination.[79] If the obligate fig wasp population is affected by changing climatic conditions, then the trees have no substitute pollinators and will fail to produce viable seeds. Investigating how pollinators of primate food trees are affected by climate change will be an important area of study.

As we suggested 20 years ago, the need to combat climate change offers a great opportunity for primate conservation. Globally, tropical forests store 55% of all forest carbon stocks and deforestation and forest degradation account for as much as 20% of the global anthropogenic greenhouse gas emissions.[57] Estimates suggest that tropical forests and wetlands could contribute 23% of the mitigation needed to stabilize global warming to below 2°C by 2030.[80,81] Currently, 20 million km^2 of forest and forest/savanna do not support sufficient agricultural productivity or effectively generate significantly needed ecosystem services, thereby representing important opportunities for restoration.[82] The potential value of forest restoration and

protection, motivated by needs to curb climate change, is an opportunity that primate conservation scientists must act on.[56]

3.2 | Disease

The Covid-19 pandemic has clearly exposed the potential impact of disease and the fact that human actions have eroded environmental resilience. As of 25 April 2021, over 147 million people had been infected by Covid-19, a virus likely originating from wildlife resident or traded in China.[83] With Covid-19 on our minds, it is easy to forget that the AIDS pandemic infected over 76 million people and originated from primates in West Africa,[84] or that the 1918 influenza virus originated from birds in Kansas and killed up to 50 million people.[85] Rates of discovery[86] and emergence of new diseases are accelerating.[87] For example, within the last decade in one small area of Kibale, distinct simian pegiviruse were discovered in three species of wild monkeys,[88] as well as a new SIV lineage in red-tailed guenons (*Cercopithecus ascanius*),[89] and novel delta-lenti-and spuma-retroviruses.[90]

The extent to which disease causes dramatic primate declines represents an area of active investigation, but this is severely hampered by the lack of long-term monitoring of primate populations over broad areas.[91] Nevertheless, there are a few well-documented examples of disease-causing population declines. For example, surveys carried out in Gabon documented a 90%–98% reduction in the gorilla and chimpanzee populations thought to be the result of an Ebola outbreak.[92,93] Similarly, a prolonged yellow-fever outbreak has been decimating non-human primate populations throughout Brazil for several years.[94]

Devastating diseases may be accelerating at a faster rate as human actions and climate change have eroded ecosystem resilience. If this is true or if the role of disease is more important than previously recognized, then many species with small population sizes are at greater risk of extirpations than previously thought. While not all diseases are necessarily lethal, there are some that can clearly devastate populations of plants and animals alike, such as Dutch elm disease and rinderpest.[95]

3.3 | Sublethal environmental contaminants

It is best if conservation scientists can identify environmental and societal change that will threaten wildlife as quickly as possible. By doing so it becomes possible to direct preventive action prior to population declines, rather than recommending remedial action after the declines have occurred. In this vein there are two issues that we think may become serious threats to primates: microplastics and pesticides. The world is producing a staggering amount of plastic, 402 million metric tonnes per year, which is the weight of 40 million buses loaded with people[96] and production is growing at 8.3% a year.[97] Over 40% of this is single use plastics.[98] Much of this ends up in landfills, however, 32% do not, and surprising amounts are found in the air we breathe and as dust that settles, in the water we drink. Microplastics became a concern in oceanographic studies about a decade ago, as large amounts of such particles were easily found floating in the water column. Researchers have recently discovered that small plastic particles are a common component of inhaled dust and contained in drinking water. Furthermore, researchers have recently appreciated the magnitude of this deposition. For example, it is estimated that 132 plastic particles per m^2, which amounts to >1000 metric tons of plastic, are deposited each year on protected lands in the western United States.[96] Atmospheric transport of these particles means that they are found in remote regions far from their sources, such as pristine mountain habitats of the Pyrenes (95 km from a source),[99] the Arctic,[100] and the Tibetan Plateau of China.[99] People consume about 39,000 to 98,000 plastic particles each year[101] and inhale between 10,000 and 100,000 particles a year.[102] How much is consumed by terrestrial wildlife is largely unknown.[101]

The effects of such plastic consumption are poorly understood, but particles move across the gut lining and are found in all major organs, with microplastic fibers bioaccumulating in the lungs and triggering inflammation.[97] These plastic particles are organic pollutants and additives found in plastics are thought to cause reproductive and developmental problems, depress the immune system, and disrupt the microbiome in the gut.[103] Quantifying the magnitude of the exposure of primates to plastics and determining the sublethal consequences of this exposure, may raise the alarm to an important issue that will negatively impact populations. In doing so, this would add voice to curb the use of plastics, and ban single use items altogether (e.g., plastic bags).

The negative effects of pesticides were first brought to the public's attention through the publication of Rachel Carson's Silent Spring in 1962.[104] Yet today there are approximately 85,000 synthetic chemicals made and approximately 2300 billion kg of pesticides are used each year.[105] Atmospheric transport then deposit pesticides in remote areas where they were never applied, such as the Arctic[106] and mountain tops.[107] Many pesticides known to have severe negative effects on mammals are banned in high-income countries but are still used in tropical countries in which primates occur (e.g., DDT).[108] Many of these chemicals have sublethal impacts on mammals and are known to disrupt the endocrine system and cause adverse developmental, immune, and reproductive effects.[109] Exposure at low levels will not result in mortality but could contribute to the extirpation of stressed populations. For example, atrazine, the world's second most widely used pesticide, is known to cause a decline in sperm production in many species and decreased fertility in humans.[105]

Research in primate habitats in Uganda and Costa Rica found significant levels of four groups of chemicals in the forest atmosphere, including legacy pesticides, currently used pesticides, halogenated flame retardants, and organophosphate flame retardants.[110] These researchers followed up on their findings and sampled dung of howler monkeys in Costa Rica, and baboons, chimpanzees, red-tailed monkeys, and red colobus in Uganda.[110] Numerous anthropogenic chemicals were found in all species. In our opinion, research examining how these synthetic chemicals directly and indirectly affect the

world's non-human primates through their synergistic interactions with other stressors, such as climate change, should be a priority. Conservation plans that incorporate the effects of microplastics and pesticides must propose preventative action as these compounds will be with us for a very long time.

4 | CONSERVATION ACTIONS

The way conservation is planned and deployed has changed dramatically in the last 20 years. One of the most positive advances is that the amount of information available to make decisions has increased substantially. When we wrote our original article in 2000 one had to rely on a relatively small number of case studies when trying to generalize. Thus, predicting how a single species in a particular location would respond to a disturbance was difficult and likely to be inaccurate.[111] To illustrate this growth of information, we enumerated the number of papers published per year on primate conservation (Google Scholar searches using the term "primate conservation" (Figure 3). In the last 20 years, the annual publication rate has increased by a factor of six. Despite substantial geographic knowledge gaps, this means that it is now possible to make insightful meta-analyses of the responses of primate populations to anthropogenic pressures and their consequences.[21,112,113]

The accumulation of information permits analyses of data gaps, which provides a roadmap for future research efforts. For example, Junker et al.[114] reviewed thousands of conservation studies and found that despite intensive efforts to study primates, less than 1% of all studies evaluated conservation effectiveness. Furthermore, many of the studies that did provide evaluations, lacked quantitative data, failed to undertake post implementation monitoring of populations or individuals, or implemented several interventions at once. The few studies reporting the needed information often revealed that the conservation approaches being used have been misguided. As a result, millions of dollars of conservation funds have largely been wasted.

One of these approaches involves Integrated Conservation and Development Projects (ICDPs). This approach has frequently been advocated as an effective and ethically appropriate tool to protect primates. It is considered appropriate as the projects strive for a "win-win" outcome in meeting the needs of both local communities and primate populations.[115–118] This perspective emerged from the 1982 World Parks Congress in Bali, where there was consensus that "protected areas in developing countries will survive only insofar as they address human concerns" (p. 134).[115] The integration of biodiversity conservation with sustainable development became a widely supported conservation strategy following the report issued by the World Commission on Environment and Development in 1987 (the Brundtland Commission[119]). This approach has been further encouraged by the development of the Millennium Development Goals. Most commonly advocated projects of this nature involve ecotourism.

Empirical evidence supporting the de facto effectiveness of ICDPs are scarce. John Oates presented early examples of failures of this approach.[120,121] In Nigeria, local farmers were allocated land after logging, provided they subsequently planted and tended timber species along with their crops, and then moved on. The offer was attractive and many people immigrated to the area and participated, but subsequently they refused to leave the land and the forest reserve was lost. A comparison of protected areas in Uganda using community-based approaches to those that did not, documented no difference in threat reduction.[122] A study in Mexico documented that co-benefits delivered through an ICDP were insufficient to reduce illegal resource extraction or counter the profit that could be made from illegal resource exploitation.[123] A review of financial incentives to curb illegal hunting, that included cases in Nepal, Kenya, Namibia, Mexico, and Sweden, concluded that the benefits provided were usually outweighed by the losses incurred by local residents, and rarely reduced illegal hunting.[124]

ICDPs often assume that if the basic needs of the local community can be met (e.g., they are provided with high protein foods), then the resource extraction in question will decrease. This assumes that local community members will be satisfied by their lot in life once their basic needs are met. We view that this ignores basic human nature—if people can further improve their lives by continuing to extract resources, they will, as these can be converted into desirable

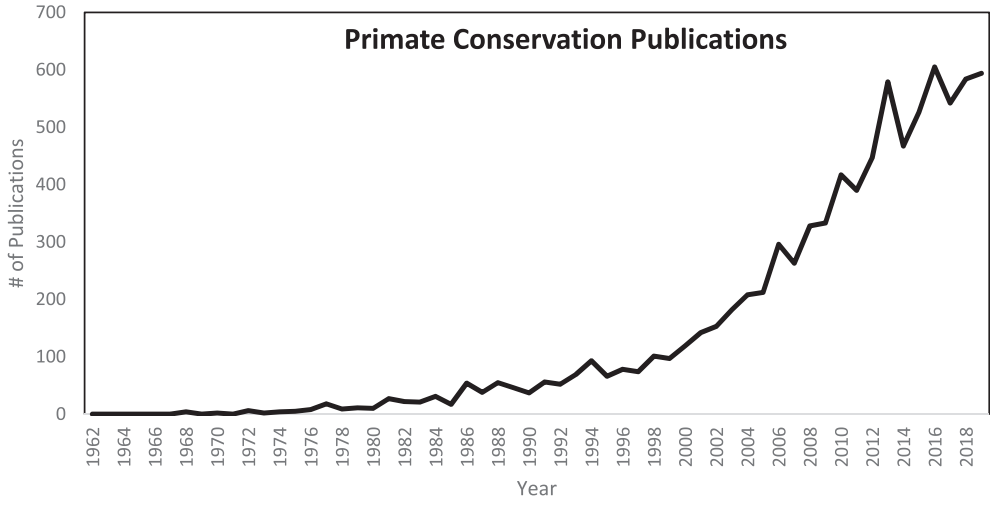

FIGURE 3 An illustration of the increase in scientific information available on primate conservation issues over the last half century. The number of papers published per year on primate conservation (Google Scholar searches using the term "primate conservation")

goods and services. This is the basis of capitalism that fuels so much of the activities of people in high-income countries. Thus, not surprisingly, some studies have found that the opposite—as conservation organizations boosted the wealth and well-being of communities around protected areas, the incidence of forest product extraction and hunting increased.[125] In Kibale, as the wealth of the community increased or as people received more employment benefits from the park, both the incidence of illegal forest product extraction and hunting increased. Rasolofoson et al.[126] examined the conservation value of Community Forest Management programs in Madagascar designed to allow local communities to benefit from resources harvested from the forest, while not degrading them. They found that these programs were ineffective and did not reduce deforestation (see Mugisha and Jacobson[122] for a similar example). More generally, Waeber et al.[127] demonstrated that, despite hundreds of millions of dollars spent in Madagascar on over 500 environmental projects, deforestation remains unchecked and efforts have failed to reduce poverty or meet any of the Sustainable Development Goals.

Let us be clear, we are not advocating conservation projects should not be engaged in assisting local communities. There are many reasons for improving the livelihoods of local communities, including important moral and ethics considerations,[118] not to mention lower levels of local resentment in implementing protection measures. However, these projects may do little to conserve wild primate populations. We are in no-way advocating returning to a fortress conservation perspective. Rather, a mixed approach is likely needed. One that balances careful, culturally appropriate law enforcement, with improving the health and livelihoods of the local people being affected. Here the overall value of each component of a conservation strategy needs to be assessed in relation to the desired goal (e.g., stopping poaching, improving the welfare of local community members, fostering positive park-people relations), and the approach must be tailored to each ecological, cultural, and economic setting.

There is evidence pointing to the importance of establishing protected areas that are effectively patrolled, thereby incurring substantial disincentives for encroachment and resource extraction. Since 1992 and the Earth Summit in Rio de Janeiro, the global network of protected areas has roughly doubled, increasing yearly by an average of 2.5% in total area.[128,129] In 2010 the 192 governments signing the Convention of Biological Diversity (Aichi Target 11) agreed to expand the system of protected areas from 13% to 17% of the planet's land surface area by 2020.[130] However, only 9.8% of the tropical forest biome, where the vast majority of primates are found, is in protected areas, and many of these areas fail to provide effective protection.[131] Analysis of satellite images suggests that 32.8% of all global protected lands are under intense human pressure, with roads, agricultural encroachment, and urban development occurring within the protected area.[129] A global analysis showed that only ~50% of 60 protected areas have been effective over the last 20–30 years, while the remainder were experiencing alarming biodiversity erosion[132] (see also Tranquilli et al.[133]). This is poignantly demonstrated in Tai National Park, Cote d'Ivoire, where primate density is 100 times higher near the protected research station and tourism site where hunting is deterred, than in the remainder of the park.[134] Overall, 13 of 23 protected areas in Cote d'Ivoire have lost their entire primate populations.[135]

There are, however, success stories where parks have been highly effective. For example, increased patrolling limited the use of snares in Kibale and corresponded to a park-wide increase in primate, ungulate, and elephant numbers.[125,136] The need for some form of patrolling enforcement has been echoed by many.[133,137] Researching how to make the largest conservation gains for primates from existing and new conservation areas is a clear research priority and will involve working closely with local communities. This is a fruitful avenue for academics to explore.

While we have come to realize that many parks are not as effective in protecting primates as we might hope, we have come to appreciate how fast some tropical forest can regenerate and become suitable habitat for many, if not most, primate species. Degraded forests in most primate host countries now exceed the area covered by undisturbed old-growth forests.[138] In fact, secondary forests now represent approximately 35% of all remaining tropical forests.[139] Baya and Storch[140] surveyed a village site in Korup National Park, Cameroon that had been abandoned for 7–8 years and found populations of all eight primate species that occur in the region; in addition sighting frequency was not significantly different from other sectors of the park.[141] Seven years after an area of grassland in Kibale was replanted with trees as part of a carbon offset program, all species of diurnal primates were present in high numbers, including the endangered red colobus and chimpanzee[142] (Figure 4). Furthermore, population densities of all six primate species in the restored area 19 years after planting, were equal to those in neighboring old-growth forest, except for mangabeys (*Lophocebus albigena*).[143] Having said that, not all primate species can thrive in even reasonably mature second-growth forests (>20 year-old) as some species are old-growth specialists and require large areas of intact primate forest to persist.[144]

We believe that tropical forest restoration must be an important tool for primate conservation in the coming decades if we are to prevent extinctions. Our emphasis on this approach stems from the fact that so many species have been reduced to small populations surviving in isolated forest fragments. While we are optimistic about the value of restoration, it is important to realize that not all disturbed forest recover. Regeneration can become arrested in some areas as herbs, ferns, and grasses inhibit canopy tree recruitment.[145,146] Understanding which forests will recover after disturbance and which will not, is an important area of study.

5 | THE NEED FOR SYSTEM CHANGE

As we did 20 years ago, here we point to system changes that we think will promote the conservation of primates and their habitats. It is pleasing to see that advances have been made with respect to ideas we promoted so long ago, humbling to see the mistakes and omissions we made, and discouraging to see that in some key areas, advances have not been achieved. Where we have not advanced, we believe

FIGURE 4 (a) The Ashy red colobus monkey (*Piliocolobus tephrosceles*) on of the endangered species that does well in regenerating forest such as that seen here (b). This particular regenerating forest follows regeneration in Kibale National Park, Uganda is only 12 years after the forest had been clear cut

the major impediment has been that the system in which we operate inhibits progress. There are seven areas where we view significant system change is required for academics to more effectively advance primate conservation. Research is needed into each of these areas to determine how to bring about change. However, while more research is needed, it is clear that we already have sufficient knowledge to take many needed actions. Thus, the call for more knowledge should not be used as a delay tactic.

5.1 | Knowledge to action pathway

One area deals with the *knowledge to action pathway*. In many instances what actions need to be deployed to conserve primates and their habitats are already known, but little or no action is taken. This is clearly illustrated by the fact that nearly 30 years ago the world's leading scientists outlined how humanity must adopt more environmentally sustainable policies to avoid environmental disasters. Yet, these warnings remain largely unheeded.[147] Barriers that prevent knowledge exchange are well documented, but finding workable solutions has been elusive.[148] Producing science that will effectively inform policy decisions and motivate action requires that the information produced be salient (relevant and timely), credible (authoritative, believable, and trusted), and legitimate in the eyes of researchers, policy makers, and agents that create action.[149] Within the science-to-action context, "communication strategies" are explicitly a part of a "political strategy." This strategy is set within a theory of change that includes an assessment of the priority audiences, what actions one wants them to take, what filters or biases they bring to how they process knowledge, who else is seeking to influence their actions, who are the effective messengers (often not scientists), and what are the effective modes of communication.[150–156] There are different ways to get messages across and different venues to deliver the content. For example, over the last decade it has become clear that presenting a positive, optimistic message (e.g., we are all in this together and we can make change happen) holds more promise in translating knowledge to action than a doom-and-gloom perspective. Research into how to effectively communicate scientific information and bring about change is a research area we view as greatly needed. Also, it would be extremely useful if graduate programs offered instructions on how to effectively communicate to a variety of audiences. We find it ironic that most graduate programs stress the need for understanding of statistics, but fail to emphasize the need for effective communication, not to mention a knowledge of natural history.

5.2 | Incentive system

Twenty years ago, we suggested that the *incentive system* entrenched within mainstream academia needed to change to promote conservation. Unfortunately, the situation has deteriorated, rather than improved, and current academic policy strongly discourages practical conservation research.[157] Academia has become even more competitive since we wrote our original article. This is illustrated by the fact that only 43.2% of all science and engineering PhDs in the United States are employed in institutions of higher education, and full-time faculty positions have declined steadily for four decades.[158] Early-career scholars face a challenging environment where time is a precious commodity that if single-mindedly invested into advancing a career, is perceived to compromise personal lives.[159] In academia, work-related anxiety or depression is common; of 4000+ scientists surveyed, 80% perceived that competition had fostered mean and aggressive behavior and half were struggling with depression or anxiety.[160] Academics are evaluated for jobs, tenure, advancement, and grants based on the rank of the journal in which they publish, the number of times they are cited, their h-index, and even their altmetric

score[161,162]—none of which are typically advanced by conducting practical conservation. Practicing critical field conservation activities, such as holding community workshops or doing abundance surveys, is often viewed as at best only nominally contributing to academic advancement. Many of these endeavors are typically defined as outreach rather than research and will be undervalued in the tenure and promotion process.[163] Thus, unfortunately, it would be logical to advise graduate students or early career scientists not to engage in these activities until after tenure and to concentrate on publishing academic papers in high impact journals.

Granting agencies, particularly foundations, are always looking for something novel and thus do not facilitate the long-term research that is needed in conservation.[91] Granting agencies thus incentivize grabbing onto fads, which is typically done without adequate testing of effectiveness or consideration of how particular field conditions would affect the outcome.[164] A current fad is to take high-tech approaches with sensors.[165] With all conservation projects, it is important that the hard-earned funds be spent in a fashion that best facilitates both science and conservation. When conservation dollars are spent on sensors, funds are going to corporations, typically in high-income countries. In contrast, when a local villager living close to the conservation efforts is hired to collect data, funds go to the community and engender a positive attitude towards conservation efforts as it ameliorates some of the negative impacts of living next to protected forests.[48,166] High tech is also being promoted to secure parks (e.g., thermal and infrared cameras, passive recorders, and software systems to detect people entering parks by the World Wide Fund and Google).[165] However, while this militarization, termed "War on Poaching" or "Green Violence," may be appropriate when dealing with well-organized international cartels, it is not appropriate when dealing with local villagers hunting bushmeat or collecting medicinal plants for personal consumption and will lead to alienation and hamper community cooperation. While universities are more strictly adhering to business models than ever before and granting agencies may like fads, it is our professional community that awards tenure and reviews grants, so it is in our purview to modify the incentive system as we see fit. We are at a loss to explain why we have not done so, when the need is clearly there.

5.3 | Training

A third way that the system needs to change deals with the *training* of primate host country scholars and practitioners. The education system in many tropical countries is struggling. With the recognition that economic growth would be knowledge driven, the early 2000s set off a flurry of expansion in higher education in many tropical countries. For example, enrolment in higher education in Africa doubled between 2000–2013,[167] but capacity (e.g., teacher number and salaries, research funding) did not keep pace. To meet this increasing student demand, professors now teach more classes, to a greater number of students, leaving little time for research and mentoring. Furthermore, in many tropical countries, low faculty salaries and highly paid short-term contracts from development agencies and conservation NGOs often results in faculty canceling classes for extended periods during the school year, to take on consultancies and make a salary they feel they deserve. It is disappointing to see conservation NGOs being a negative contributor to university training in this way. In addition, much of the professoriate in many tropical countries has limited training in research,[168,169] particularly when it comes to new, often expensive laboratory methods (e.g., genetics or hormone analysis) or software (e.g., remote-sensing platforms, GIS). In Ethiopia, for example, though graduate degree holders are on the rise, less than 20% of university instructors hold Master's degrees and fewer than 6% hold PhDs.[170] The gulf between students clamoring for science education and the infrastructure and personnel to nurture that demand is also growing in emergent economies such as Brazil.[171]Without a critical mass of doctorates among the faculty, how will doctoral students be adequately trained?

The current incentive system in most high-income countries makes it disadvantageous to train primate host-country students.[172] Such students may require additional time to obtain training, are more likely to publish on local issues in low-impact journals, and often require additional expenses that must be met by their mentor, all of which make them less advantageous with respect to the incentive system at universities. It is our opinion that universities in higher income countries have failed to provide the atmosphere that would encourage professors to invest their limited energy and resources in training graduate students from the 90 (mostly tropical) primate habitat countries. Thus, it is well past time that the reward system of universities in higher-income countries change to meet the reality of a global society. These hurdles are not insurmountable: after all academic institutions largely control their own incentive systems. Imagine how the rate of training would change if every paper published by a primate-host country graduate student supervised by a researcher from a high-income country counted twice as much for tenure and promotion.

5.4 | Long-term and spatially widespread ecological research

The fourth issue where system change is required to promote primate conservation concerns the need for *long-term and spatially widespread ecological research*. A central goal of conservation research is to understand the drivers of population change. This requires identifying a signal that is greater than stochastic variation caused by minor ecological or demographic variation, events that are largely stochastic (e.g., the appearance of a predator in an area), and sampling error associated with having only a few time points to estimate population change.[173,174] This necessitates long-term ecological research that is spatially spread over the conservation area, rather than just the habituated individuals neighboring a single field camp. In the past primate research has focused on behavioral and socio-ecological research studying single groups and little attention has been given to detailed ecological quantification. While such research is valuable to address

many theoretical questions, it does not generally provide the information needed to construct informed conservation plans.

5.5 | Shift in perception of conservation work

The fifth way we see the system needing change is the need for a shift in perception of conservation work among high-income country scientists, and an explicit acknowledgement that conservation cannot be separated from the ethics of improving the lives of people in primate host countries, nor can helping people simply be a means to the end of conserving primates. In the end, conservation must come from within the primate host countries. Ownership of conservation must rest with the people who ultimately bear the costs and reap the benefits of conservation—stakeholders include communities, national governments, and others who hold rights over the natural resource base.[175] While the benefits will be reaped globally, these are the institutions, groups, and people who must make the long-term investment. Without their dedicated sacrifice, we do not believe that significant, long-term protection of primate communities and habitats is possible.

5.6 | Evaluation of conservation

The sixth issue deals with the *evaluation of conservation*. For conservation to be effective, we must learn from both successes and failures of past attempts to protect primates. Most, if not all, conservation efforts require substantial time to detect an effect. Some efforts require decades before we would expect results, such as conservation outreach targeting children. Despite this clear need, appropriate long-term evaluations are very rarely done. Obtaining long-term data on primate populations, ecological variables that could drive change, and the effectiveness of conservation approaches requires consistent funding over at least a decade. Creative ways to fund projects over such long periods need to be explored. One avenue to do this is through the creation of research teams participating in more collaborative funding endeavors that ensure consistent funding of monitoring efforts—this is the last issue we wish to raise.

Without appropriate evaluations, there is no way that conservation projects or scientists can be held accountable. This enables agencies, groups, and individuals that continuously underperform or fail to continue largely unquestioned and there being limited accountability with respect to expenditures, including salaries. Let us relay a sad example from Kibale. A large conservation group held a 6-year, multimillion-dollar grant and two of their primary goals were to protect biodiversity and reduce domestic fuelwood consumption by promoting fuel-efficient stoves and thereby alleviating the need to collect fuelwood from the park. At the end of the granting period the group had not measured any indices of biodiversity, and thus asked long-term researchers for data to show they were effective. Subsequently, it was found that there was no difference in fuelwood consumption between the stove design they were promoting and what was originally used by the community.[176] Without meaningful long-term accountability, it becomes very easy for conservation groups and scientists to build seemingly impressive personas by essentially "shouting louder" than others.

5.7 | Creation and coordination of teams and networks

The last issue where we view system change is required deals with *the creation and coordination of teams and networks*. Given the current threats primates face and the recognized knowledge gaps, there is a clear need to accelerate the process of scientific discovery and gather, coordinate, and empower networks containing multidisciplinary teams of international collaborators. We need to leverage research and educational resources to tackle the challenges of primate conservation, which requires significant coordinated international efforts. Networks of scholars and practitioners should promote synergies to provide innovative solutions and professional development for early-career researchers across that globe. Well-meaning academics and conservation groups frequently initiate small-scale conservation projects but fail to coordinate actions. This results in conflicting information being relayed, community hopes being dashed as projects make large claims that are rarely met or maintained, and intense competition for funding. NGOs are spending a larger portion of their budgets hiring grant writers and administrators, while progressively engaged in fewer and fewer long-term conservation efforts of the types needed.

Researchers and practitioners need to coordinate to send a clear message to funders regarding conservation priorities, including species, sites, and approaches. In the last 20 years we have repeatedly seen funding agencies push projects "using a one size fits all" approach. For example, based on a program in the Amazon (rural population density < 2 people/km^2), funding was allocated to a large project in Uganda to allow access to a park by a community numbering almost 200 people/km^2, and lacking the means to regulate activities once access was granted—a remedy for disaster. With the sharing of information and coordination of efforts, the chances of success will increase greatly.

6 | CONCLUSION

The goal of this paper was to consider what two decades has meant for primate conservation and we sought to use this evaluation as a springboard to guide future research and actions. Over this period, the threats to primates worldwide have become even more severe. But the tools and knowledge we can wield to improve the situation has grown substantially. The most important message we want to relay is that the motivation for conservation must be strengthened if societies are to exert the political will to make the necessary changes. If we do not act soon the will for positive action will diminish. Each generation describes the environmental conditions that they consider normal. Evidence suggests that across generations there is a progressive downgrading of what is normal and thus what conservation

targets should be—a phenomenon called "shifting baselines".[177] Evidence suggests that this progressive downgrading is associated with a loss of people's affinity for nature,[178] without which engagement in pro-environmental actions declines.[179] In Uganda, an extremely small percentage of the youth will ever experience the wonders of the country's forests, while in Brazil, the most urbanized country in the Americas, children have become increasingly divorced from nature, even though the country supports about a quarter of the world's primates and half of all remaining tropical forests. It is likely that conservation scientists starting their careers today will set as their goal to conserve what primate habitat that exists today. They will not appreciate the extent of what has been lost in the last few decades, and if they accept the proportional losses that scientists starting 20 years ago have seen, the following generation will have little left to conserve.

Almost 60 years ago, François Bourlière asked whether society can remain unmoved by the annihilation of primates and their habitats—today we ask the same question but framed slightly differently. Do we have the will to prevent widespread primate annihilation and extinction?

ACKNOWLEDGMENTS

We thank Pengfei Fan, Himani Nautiyal, Claire Hemingway, and Mitch Irwin for helpful comments and insights they provided.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable as this is a review article and no new data were created or analyzed.

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How to cite this article: Chapman CA, Peres CA. Primate conservation: Lessons learned in the last 20 years can guide future efforts. Evolutionary Anthropology. 2021;30:345–61. https://doi.org/10.1002/evan.21920