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Perspectives on Conservation Impacts of the Global Primate Trade

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Abstract

The global trade in nonhuman primates represents a substantial threat to ecosystem health, human health, and primate conservation worldwide. Most of the primate trade involves trade for pet-keeping, consumption, or biomedical experimentation. We present an overview of international primate trade through five case studies; each describes a different facet of this trade. We draw on published scientific literature, media outlets, and open access datasets, including the CITES Trade Database to build these case studies. Case study 1 describes the role of introduced island populations of *Macaca* and *Chlorocebus* in trade for biomedical experimentation; case study 2 covers the global health threats posed by the primate trade, including zoonotic disease transmission once animals enter the trade pipeline; case study 3 addresses the ways that changing patterns of primate trade, from local markets to online, have increased the demand for primates as pets; case study 4 recognizes the role that local environmental activism can play in mitigating trade; and case study 5 shows variation between global regions in their contribution to the primate trade. We recommend greater oversight of primate trade, especially domestic trade within primate range countries, and real-time reporting to CITES to accurately track primate trade. Effective conservation-focused regulations that can minimise the negative effects of primate trade

Badge earned for open practices: Open Data and Open Code Badges. Experiment materials and data are available in the repository at https://github.com/GalB96/Perspectives-on-the-Global-Primate-Trade.

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must be tailored to specific regions and species and require transparency, careful regulation, field research, and an understanding of the magnitude of this trade.

Keywords CITES · Conservation data deficiencies · Monkeys · Trade · Wildlife crime

Introduction

The extraction of other-than-human primates (primates hereafter) from their ecosystems, whether for use as pets, consumption, traditional medicine, or use in biomedical experiments, is a substantial concern for their conservation, and several large-scale investigations have shown that the trade in primates adversely impacts free-ranging primate populations (Estrada *et al*., 2017, 2022; Nijman *et al*., 2017; Fernández *et al*., 2022). By free-ranging, we mean that all primate populations that are not restricted in movement by human-made barriers designed to confine animals to specific locations. The removal of seed-dispersing and pollinating primates from ecosystems negatively affects the growth and demography of plants that other animals rely on for food (Estrada *et al*., 2017). In addition, many primates have great cultural significance for indigenous human communities (Lambert, 1998; Koné *et al*., 2008) with whom they share their natural habitats and removing primates from these habitats could negatively influence indigenous cultures (Fuentes, 2010; Hansen *et al*., 2021; Estrada *et al*., 2022). Other studies have identified additional negative ecosystem effects, including reduction in carbon sequestration and changes in predator-prey relationships, when primates disappear from the landscape (Morton *et al*., 2021; Estrada *et al*., 2022; Harvey *et al*., 2023). The removal of primates from their native environments can result in alternative zoonotic pathogen reservoirs in human populations that could potentially start new human epidemics and pandemics. Without stable reservoirs previously sustained in primate populations, these pathogens are more likely to enter and spread in human populations (Wolfe *et al*., 2007; Devaux *et al*., 2019; Borsky *et al*., 2020; Hamers *et al*., 2023; Campbell *et al*., 2022). Once in the trade pipeline, primates are rarely (if ever) provided with adequate living conditions and regularly experience unhealthy levels of stress that further exacerbate disease outbreaks (Roberts & Andrews, 2008) and raise serious concerns about the ethics of this trade and its implications for animal welfare (Travers & Turner, 2005; IFAW, 2008). The global primate pet trade, propagated via the internet (Soulsbury *et al*., 2009; Siriwat *et al*., 2019; Nijman *et al*., 2021), and an increasing demand for free-ranging and captive-bred primates for biomedical experimentation, worsen the primate conservation crisis (Maldonado *et al*., 2009; de Souza Fialho *et al*., 2016; Subbaraman, 2021; Svensson *et al*., 2023).

The primate trade is a global industry. The estimated market value of legal exports of just one species of primate, the long-tailed macaque *Macaca fascicularis*, from ten countries from 2010–2019 was USD 1.25 billion (Hansen *et al*., 2022b). However, tracking the trade in primates globally is difficult, as much of the trade happens within countries and some of the trade (domestic and international) is illegal and therefore undocumented (Norconk *et al*., 2020; Hansen *et al*., 2021, 2022a).

It is particularly challenging to track the domestic trade within primate range countries, whether for biomedical and pharmaceutical research, primate meat, pets, or traditional medicine, because in most cases this is not documented. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which went into effect in 1975, is a binding international agreement among parties that regulates and documents wildlife trade (CITES, 2022). Member states of CITES are expected to report their yearly international export and import of CITES-listed species no later than November of the following year (CITES, 2022). These annual reports make it possible to track the numbers for legal, international wildlife trades, and can be a helpful tool for research into the impact of trade on wildlife populations (Nijman *et al*., 2011; Estrada *et al*., 2017; Hansen *et al*., 2022b), although legal CITES-regulated trade may not result in sustainable harvest of wildlife (Hughes *et al*., 2023). In addition to legal domestic and international trade, there is an unknown level of illegal trade. Examples of illegal trade include trade that is in clear violation of one or more pieces of domestic or international legislation or trade that only partially meets the requirements for legal trade (i.e., when primates are traded for reasons other than those for which permission was granted) (Warne *et al*., 2023).

To understand the impact of the trade on free-ranging populations, it is important to identify the country of origin, because primates can be reexported. Reexport is defined as the export of primates who were previously imported into the exporting country from other countries (CITES, 2022). It also is important to determine whether individuals are captive-bred or wild-caught, and whether captive individuals are defined as captive-born F1 (first generation, born in a captive setting) or captive-bred F2 (second generation or above, with both parents having been born in a captive setting). The EU now requires all imported primates to be at least F2, potentially reducing its impact on free-ranging populations.

Primates are traded globally for three primary reasons: as pets, for consumption (including for food and medicinal purposes), and for laboratory experimentation. Primates are sourced either directly from free-ranging populations—as is most often the case for the bushmeat trade (Nuñez-Iturri & Howe, 2007; Hicks *et al*., 2010; Covey & McGraw, 2014; Cronin *et al*., 2017) – or from breeding farms, as is mostly the case for primates used in laboratory research. Once in the trade, they may be transported within domestic markets or exported into international markets. Although domestic markets often are harder to track, because they are less likely to produce trade records making it difficult to generate quantitative estimates, international trade in specimens and products can be equally difficult, especially when illegal (e.g., the trade in primate parts into Europe; Svensson *et al*., 2023).

All primate species are listed on either CITES appendix I (which lists species for which commercial international trade in wild-caught individuals is prohibited) or appendix II (which lists species for which international trade is regulated) and require CITES export permits. Some species also require import permits (all appendix I species, in addition to primates imported into specific countries that have put in place more stringent measures). However, there are frequent discrepancies in reports of imported and exported primates from each country. It is likely that a proportion of individuals traded and listed as captive-bred are actually wild-caught because of falsification and mislabelling of records on CITES permits (SSN, 2012, 2015a,

2015b; U.S Attorney's Office, 2022; Warne *et al*., 2023). Moreover, because trade in wild-caught primates is illegal in many regions, sellers are incentivised to misrepresent the number of primates captured from wild populations and claim that they are captive-bred. This makes it difficult to assess the level of threat to wild primate populations (RFA, 2023; Delgado, 2023; Warne *et al*., 2023).

Our goal is to provide readers with accurate and reliable information to better comprehend the magnitude and diversity of the primate trade. There is no single available database that documents all aspects of the primate trade. Even where data are available, data on domestic trade, whether legal or illegal, disease transmission associated with primate trade, online trade, and the quantitative impact of Nongovernmental Organizations (NGOs), are not reported in a standardized way. Therefore, we examine the global primate trade through five case studies that draw on published literature and data from academic papers, media reports, government or legal reports, and (where possible) data from the CITES Trade Database. We begin by discussing four prominent issues within the global primate trade; namely trade in introduced primates (case study 1), the public health risks arising from the primate trade (case study 2), the role of the internet in the primate trade (case study 3), and the role of environmental activism in combating the illegal primate trade (case study 4). The final case study (case study 5) uses the CITES Trade Database, for the period between 2010–2022, to illustrate patterns of reported trade across primate species, regions, and purposes. These case studies represent examples of the wide-ranging impact that the primate trade has on several, disproportionately affected, primate species and the human-primate interface.

Case Study 1. Trade in introduced primates

We exemplify the trade in introduced primates through the trade of *Chlorocebus sabaeus* and *Macaca fascicularis* from islands in the American tropics (St. Kitts, Nevis, and Barbados) and Africa (Mauritius), respectively. The islands of St. Kitts, Nevis, and Barbados have been home to *Chlorocebus sabaeus* (African green monkeys) since the 1600s, when the monkeys were transported by colonists and merchants from West Africa to the Caribbean (Dore, 2017). A recent study estimated that some 30,000 *Chlorocebus sabaeus* inhabit St. Kitts (which is 168 km^2) (Dore *et al*., 2023). While the islands have unique histories, topographies, and land use patterns that impact the dynamics of their respective human-monkey interfaces, problems with monkeys and negative perceptions of them have increased dramatically on all three islands to the point where they are now locally considered an invasive species. These monkeys are viewed as pests because of their consumption of local crops; they were officially declared as vermin in Barbados in 1682 (Dore, 2017), and bounties have been established for culled monkeys on all three islands in recent years. While detailed data are only available for St. Kitts and Nevis, these reports show substantial negative impact to the islands' local economy and food security, with monkey crop damages amounting to one million USD annually (Dore, in prep).

As a result of their abundance and bad reputation, and the local pressure for monkey control, *Chlorocebus sabaeus* are harvested for use in biomedical research (Jasinska *et al*., 2013). Because of their perceived overabundance and lack of

diseases, the Behavioural Science Foundation was established on St. Kitts in 1968 to use the *Chlorocebus sabaeus* population in research. In 1976, an export market was developed for polio vaccine production. In 1982, a second biomedical research facility, the St. Kitts Biomedical Research Foundation, was developed increasing the supply of healthy animals. Monkeys are still trapped today by using a technique developed in the 1970s by Mr. Joseph Cabey, by which as many as 20–30 animals can be trapped in a single cage at one time (Dore *et al*., 2023).

Today, most monkeys trapped on the islands are used in local facilities, because exporting monkeys from these islands is challenging. If shipped, private charters are used, which is expensive compared with commercial airlines. In the past 10 years, 3,361 *Chlorocebus sabaeus* were shipped from St. Kitts and Nevis to the United States, and 827 monkeys were shipped from Barbados to the United States (U.S. Centers for Disease Control and Prevention, 2023). These monkeys were primarily wild-born and shipped after a quarantine period of at least 32 days. Recent exportation figures indicate that 0.3%–1.8% of the island's monkey population is exported each year.

A similar case is observed in Mauritius, another relatively small island (1,900 km^2), where colonists introduced *Macaca fascicularis* in the 1600s (Sussman & Tattersall, 1981). As with the *Chlorocebus sabaeus* in the Caribbean islands, *Macaca fascicularis* are seen as posing ecological threats to the island's natural flora and fauna (Sussman & Tattersall, 1981; Gumert, 2011; Sussman *et al*., 2011). For the past decade at least, Mauritius has been one of the leading global exporters of *Macaca fascicularis* (Hansen *et al*., 2022a, 2022b), many of which are wild-caught (CITES Trade Database, 2022). Due to a potential founder effect, in which a bottleneck increases genetic homogeneity in introduced populations, low genetic diversity of the Mauritius *Macaca fascicularis* also makes them sought-after for biomedical research (Kawamoto *et al*., 2008). The free-ranging population on Mauritius is estimated to have decreased from 40,000 in the 1980s to 10,000 in just three decades in response to human management efforts (Sussman *et al*., 2011). Trade in wild-caught individuals is substantial when primates originate from introduced populations (CITES Trade Database, 2024); however, introduced or not, other risks remain with capturing, transporting, and using wild-caught primates for research: for example, the transmission of zoonotic diseases to humans and the poor welfare of trapped and exported animals.

Case Study 2. Public health risks of primate trade

Capture and trade in primates can cause: 1) transmission of pathogens between humans, primates, and other animals (Pereira *et al*., 2022; WCMC, 2022); 2) introduction and spread of pathogens in captive and noncaptive primate populations (Oliveira & Santos, 2023); and 3) risks to primate ecosystem health after removal of keystone primate species (Peres & Michalski, 2006; Gamalo *et al*., 2023).

Just before the global Severe Acute Respiratory Coronavirus 2 (SARS-CoV-2) pandemic, in an effort to characterize the risk of spillover events associated with particular species, scientists assessed the presence of zoonotic viruses in mammals

and concluded that only a fraction of mammalian species harbor zoonotic viruses. Among that select group, rodents, bats, and primates accounted for three quarters of the zoonotic viruses that had been described (Johnson *et al*., 2020). Subsequently, researchers interested in the inherent zoonotic disease risks associated with international animal trade used the CITES database, coupled with recent analyses by Johnson *et al*. (2020), determined that trade in two primate species—*Macaca fascicularis* and *Macaca mulatta*—carried the greatest potential for zoonotic disease (Borsky *et al*., 2020).

On multiple occasions over the past three decades, primates imported into the United States as part of the biomedical trade have arrived with pathogens capable of causing the next global pandemic, including filoviruses and *Burkholderia pseudomallei* (Jahrling *et al*., 1990; Roberts & Andrews, 2008; Taetzsch *et al*., 2022). Primate immune systems struggle to withstand the stress of capture and exposure to pathogens while in captivity and transit, and individuals frequently become ill from pathogens that their immune systems would normally contain (Roberts & Andrews, 2008). Further demonstrating these risks, a recent publication documented the presence of zoonotic pathogens, including *Yersinia*, *Shigella*, *Campylobacter*, *Salmonella*, and *Mycobacterium*, among macaques recently imported for use in primate experimentation (Johnson *et al*., 2022). The authors reported that these animals were infected despite having cleared the Centre for Disease Control and Prevention (CDC) mandatory quarantine in the United States. In 2022, primate laboratory workers were referred for treatment for tuberculosis exposure following contact with imported *Macaca fascicularis* who had been transported to Michigan after having been released from the CDC-mandated quarantine in Florida (Hicks, 2023).

Pathogens not only threaten human and primate health, but they also introduce variability and unreliability into biomedical research, compromising experimental data from these animals (Weston, 2023). Testing protocols for specific infectious diseases are not always reliable, particularly the tuberculin skin test assay used to screen monkeys during CDC-mandated importation quarantine (Yee *et al*., 2022). Furthermore, some vaccinations administered to primates before transit also can interfere with testing protocols for other diseases. For example, the measles vaccine reduces the response to tuberculin—a protein used to test for tuberculosis (TB)—for up to 28 days (Panarella & Hursh, 2022).

In 2019–2022, the number of imported primates who were dead on arrival in the United States or who died or were killed during the mandatory 31-day quarantine increased by more than 100% (2018 fiscal year N = 66, 2021 fiscal year N =136) according to public CDC records obtained by PETA (Supplementary Information ESM 2). The CDC confirmed that between 2010 and 2020 no confirmed cases of TB were detected in shipments undergoing mandated quarantine (Supplementary Information ESM 3; Swisher *et al*., 2024). But from 2021 to 2023, at least ten shipments contained monkeys who were confirmed infected with TB (Swisher *et al*., 2024), including a strain of the disease that originated in monkeys from Southeast Asia and was never before seen in animals imported into the United States. One shipment reported that 4.8% (N = 26/540) of the animals were confirmed positive with this novel strain of TB, the highest percentage of animals infected ever recorded by the CDC (Swisher *et al*., 2024). In July 2023, the CDC issued a veterinary health alert

to stakeholders, including the Association of Primate Veterinarians, National Association of Animal Health Officials, the National Association of State Public Health Veterinarians, and all CDC-registered primate importers, stating that "While the majority of imported NHP [Non-Human Primates] with TB infection were identified and euthanized during CDC-mandated quarantine, some were detected after the NHP had been released from quarantine. Infected NHP identified post-quarantine included *Macaca fascicularis* imported from Mauritius and Southeast Asia between 2020 and 2022. These cases were identified 5 months to 2 years after NHP were released from quarantine and had epidemiologic links to other TB cases in imported NHP. MTBC [Mycobacterium tuberculosis complex] species isolated from imported NHP during and after CDC-mandated quarantine included *M. bovis, M. caprae, M. orygis*, and *M. tuberculosis*." (ESM 2, pp 1-2).

The preparation and transportation methods used to move primates across borders, along with ineffective quarantine and testing techniques for imported primates, may exacerbate the risk of disease outbreaks in exported captive populations and reduce the probability of diseases being detected during quarantine. This was demonstrated when 216 of 360 *Macaca fascicularis* imported from Cambodia into the United States in 2020 and 2021 arrived infected with *Burkholderia pseudomallei*, a bacterium classified as a Tier 1 Select Agent in the United States and the causative agent of the often-fatal disease melioidosis (Taetzsch *et al*., 2022). CDC-mandated quarantine failed to detect all of the infected monkeys (Taetzch *et al*., 2022).

Disease transmission will always be an underlying risk in international animal trade; however, several steps may be taken to reduce this risk. Ending the use of wild-caught individuals in trade and laboratory experimentation and focusing on captive-bred, habituated, and trained primates will reduce the stress experienced by animals during transport and captivity and can help to limit immune system suppression, thereby reducing the likelihood of infection. Additionally, quarantine protocols must be informed by the risks associated with transporting and processing individuals from specific regions according to the pathogens present in the exporting and importing countries and the efficiency of disease testing (United States Government Accountability Office, 2023).

Case Study 3. The global change in trade patterns: Going from physical to online markets for pet trade

For most of the last century, in many parts of the world, the place to buy a pet monkey would have been the local pet shop or the local wildlife market (Duarte-Quiroga & Estrada, 2003; Travers & Turner, 2005; Nijman *et al*., 2017). This is still the case in many places, particularly in countries where primates are native or, in more recent times, where primates are bred specifically for the domestic pet market. For international trade, a restricted number of well-connected companies shipped almost exclusively wild-caught primates around the globe; traders sourced primates from their specific trade networks and individual contacts. As internet access has become increasingly widespread, trade has shifted dramatically toward an online market, both internationally and domestically (Bergin *et al*., 2018; Nijman *et al*., 2019;

Siriwat *et al*., 2019). With the recent popularization of e-commerce and increased access to the internet, suppliers and sellers are provided with an unprecedented connection to potential new consumers and expanding markets.

In the early-to-mid 2000s, the first published studies specifically addressing the online trade in primates showed that offers of primates for sale were made in classified advertisements, on auction sites, and on specialists' websites (Travers & Turner, 2005; IFAW, 2008). However, these studies were short in duration and focused on Europe and North America (Travers & Turner, 2005; IFAW, 2008). In recent years, more insight into the online trade in primates has been gained through longer and more systematic studies, either focused on specific taxa (e.g., slow, slender, and pygmy lorises *Nycticebus*, *Loris*, and *Xanthonycticebus*: Kitson & Nekaris, 2017; Morgan & Nijman, 2020; Musing *et al*., 2015; *Macaca sylvanus*: Bergin *et al*., 2018; apes: Nijman *et al*., 2021) or all primates (Seaboch & Cahoon, 2021; Zainol *et al*., 2018; Nijman *et al*., 2023).

Despite many social media platforms specifically banning the sale of live animals or the sale of globally threatened wildlife, sites such as Facebook and Instagram have emerged as significant platforms where this trade takes place (Malaysia: Krishnasamy & Stoner, 2016; Thailand: Siriwat *et al*., 2019; Indonesia: Nijman *et al*., 2021; Philippines: Gomez *et al*., 2022; South Africa: Shivambu *et al*., 2021; Brazil: Wyatt *et al*., 2022). A wide range of species are offered for sale over the internet, but marmosets, tamarins, capuchins, squirrel monkeys, lemurs, galagos, and slow lorises—generally some of the smallest primate species—appear most frequently for sale (Table I). These are often, but not always, captive-bred within

Table I Asking prices (mean ± SD, in USD) of primates offered for sale online. Values in italics refer to taxa that occur naturally in that country. Corruption perception index runs from 1 (very clean) to 187 (highly corrupt). We obtained these data through a literature review used for Nijman *et al*., (2023) which included any literature published before 2020 as well as market surveys (Nijman, personal observation). We obtained GDP and Corruption perception index for 2019 from the World Development Indicators (World Bank, 2019) and Transparency International (Transparency International, 2019) respectively. We obtained Internet penetration for 2020 from Internet World Stats (Miniwatts Marketing Group, 2020)

Country	Internet penetration (%)	GDP (capita), USD	Corruption perception index	Marmoset	Capuchin	Slow loris
Thailand	81.7	19,228	101	789 ± 94	945 ± 669	*70 ± 24*
Japan	93.8	43,236	20	-	-	6,490 ± 3,054
South Africa	55.0	12,999	70	330 ± 30	199 ± 30	-
Malaysia	81.4	29,526	51	301 ± 70	284 ± 74	*139*
Russia	80.9	29,181	137	3,289 ± 2,082	2,652 ± 2,360	2,652 ± 766
Brazil	70.7	15,259	106	*104 ± 23*	*685 ± 216*	-
US	95.6	65,281	23	4,860 ± 439	11,225 ± 3,070	-
Indonesia	62.6	12,302	85	2,542	-	*27 ± 12*
UK	94.9	48,710	12	770 ± 125	1,700 ± 2,425	-
Denmark	97.8	59,830	1	950 ± 70	-	-

the countries where they are offered for sale, especially where the sale of (nonnative) primates as pets is legal (e.g., some states in the USA (Norconk *et al*., 2023), Thailand, South Africa, United Kingdom, Denmark). In other countries, such as Indonesia, Malaysia, and the Philippines, sellers continue to illegally offer wild-caught native species. In a recent global analysis assessing the ease of buying a pet primate online, the best predictors were the internet penetration rate (i.e., the percentage of the total population of a given country or region that uses the internet; below a certain level it is economically not feasible to move from brick-and-mortar markets to online markets) and the human-development index (possibly reflecting purchasing power, internet access, and operational logistical networks), but not the corruption perception index, GDP (Gross Domestic Product) per capita, or primate richness (Nijman *et al*., 2023).

The ability to purchase products or services online is dependent on the internet penetration rate and the infrastructure in place to distribute live animals rapidly from sellers to buyers. In the coming years, more and more countries are expected to increase their internet infrastructure allowing e-commerce to flourish. This will include many primate range countries that, hitherto, have been constrained. We expect that this will lead to a concomitant shift of the primate pet trade from traditional to online markets. The engagement of national and international officials and NGOs is crucial to monitor the trade and protect free-ranging primate populations.

As the online trade in primates for personal use (such as pets) grows, social media companies—who have become the primary markets for this trade—and governments must enforce stricter protocols for monitoring and reporting illegal primate trade online. These protocols could involve more efficient methods for identifying falsified export/import permits, and additional strategies to recognize online advertisements for primate sales. Beyond their use as trading markets, the images and videos shared on social media platforms (e.g., of humans caring for primates or primates dressed in human clothes) have been shown to increase the demand for primates as pets (Cheyne *et al*., 2022; Norconk *et al*., 2020; Social Media Animal Cruelty Coalition [SMACC] 2022, 2023; Waters *et al*., 2021). Social media platforms can therefore set and enforce specific guidelines for the type of primate-related content that can be posted (Waters *et al*., 2021). Finally, while governments can impose stricter restrictions on primate pet owners, including the requirement of specific permits to keep primates, we recommend prohibiting primate pet keeping as a more effective strategy given the current failure of governments and international organizations in enforcing permit systems and recognizing forged documents. Some countries in the European Union have already banned the use of primates as pets altogether because of the welfare concerns of keeping primates in human environments, the conservation implications of removing primates from their wild populations to supply a pet trade, and the risks of zoonotic disease transmission associated with the close contact between human and nonhuman primate pets (Food and Agriculture Organization of the United Nations, 2022). This movement may have to include financial sanctions to pressure noncompliant companies to invest in effectively combating wildlife crime (Morcatty *et al*., 2022; SMACC, 2022; 2023).

Case Study 4. The role of Environmental Activism in combating illegal primate trade, exemplified by the night monkey trade in Colombia

The global primate trade puts increasing pressure on free-ranging primates, for many of which population estimates are inaccurate (Wessling & Surbeck, 2023). For the period 1975 to 2018, CITES reported that 66% of legally traded live *Aotus* spp. (night monkeys) were sourced from range countries, where 33% of all exported live individuals were wild-caught from Peru (*Aotus vociferans* and *Aotus nancymaae*) (Shanee *et al*., 2023). These were mainly traded for commercial or scientific purposes. Among individuals from range countries (N = 123 individuals, including dead animals, parts, or derivatives), *Aotus nancymaae* were the most common (40%), followed by *Aotus vociferans* (24%) (Shanee *et al*., 2023). From 2007 to 2008, some 4,000 wild-caught *Aotus* spp. were illegally traded across the Brazil-Colombia-Peru border (Maldonado *et al*., 2009; Maldonado & Peck, 2014; Maldonado *et al*., 2023). In some cases, *Aotus nancymaae* and *Aotus vociferans* were captured under permits from environmental authorities and used for biomedical research (such as unsuccessful vaccine development: Graves & Gelband, 2006; Goyes, 2015) and then released back into the wild (Maldonado *et al*., 2009; Maldonado & Lafon, 2017; Maldonado *et al*., 2023; Maldonado & Peck, 2014). Lack of health assessments and follow-up studies post-release makes it impossible to determine the effect of capture, translocation, and potentially introduced diseases on the survival of released animals, as well as the impact of these translocations on the stability of free-ranging populations whether by introducing human-associated pathogens or disrupting demography or natural disease cycles (Nichols *et al*., 2017).

In 2014, the Colombian Research Funding Agency (COLCIENCIAS), granted approximately USD 1.2 million to Foundation Institute of Immunology of Colombia (FIDIC) (Maldonado & Lafon, 2017) after their SPf66 malaria vaccine was declared "inactive" by the World Health Organization with only 26% effective protection (Graves & Gelband, 2006; World Health Organisation, 2006). Following these findings, the local conservation NGO, Entropika, started a long-term legal and media battle resulting in policy changes by local indigenous authorities, who no longer granted trapping permits, and changes to national laws for regulating wildlife extraction (Gil-Botero, 2013). Today, the FIDIC facility in Leticia (Colombia) is closed for contravening the obligations of their latest permit (Wolovich *et al*., 2024), and in March 2023, Corpoamazonia, the regional environmental authority granting trapping and research permits, ruled against FIDIC for exceeding its annual extraction quota in 2010, applying economic and administrative sanctions (Corpoamazonia, 2023).

In another example of illegal use of primates, the biomedical facility Foundation for Primate Center Caucaseco (FUCEP), in Valle del Cauca (Colombia), began malaria research in 2001 using *Aotus* spp. (night monkeys: *Aotus griseimembra* and *Aotus lemurinus*) and *Saimiri* spp. (squirrel monkeys) (Arévalo-Herrera *et al*., 1998). FUCEP has received USD 17 million from the National Institute of Health U.S. since 2003 (Cambio, 2023). On February 17, 2023, the specialist group against animal abuse, Gelma (Grupo Especial para la Lucha contra el Maltrato Animal), which is part of the Prosecutor General (GELMA-FISCALIA) and environmental authorities,

confiscated 108 night and squirrel monkeys from FUCEP. This facility was closed for conducting illegal and unethical research and for animal abuse (CVC, 2024).

Both cases exemplify how environmental activism supported by legal actions and research can expose illegal primate trade and biomedical research and protect endangered primates. Entropika monitors and campaigns against wildlife trafficking between the Colombia-Brazil-Peru Amazonia borders, collaborates with policy makers (Senators) to improve environmental law enforcement, and provides evidence for the revision of laws related to wildlife use in Colombia (Gil-Botero, 2013). A good example of collaboration between stakeholders and primatologists is the inclusion of *Aotus nancymaae* in the list of threatened species for Colombia and the upgrade of its IUCN category from Vulnerable to Endangered (MADS, 2024). Entropika also conducts capacity building and educational programs for indigenous communities to provide them with alternatives to wildlife trafficking (Wolovich *et al*., 2024; Sollund & Wyatt, 2022), highlighting that wildlife cannot be protected unless the people are provided with both economic alternatives and improved living conditions (Sollund & Wyatt, 2022). Their impacts demonstrate that local NGOs can help guide conservation agencies and management authorities and pressure trading companies and laboratories. Importantly, local NGOs may have strong connections with local communities and stakeholders, which may facilitate better outcomes through community engagement in conservation efforts (Estrada *et al*., 2022). Domestic trade is not reported anywhere, making it difficult for policy makers and conservationists to assess the true threat to free-ranging populations and respond accordingly. An open access database, where NGOs and local enforcement agencies report confiscations, as well as the domestic trade, would greatly improve our ability to track these illicit trades and assess their impacts on free-ranging primate populations.

Case Study 5. Overview of global international trade in live primates using the CITES Trade Database

While NGOs and activism can be effective in combating illegal primate trade at a local scale, it also is critical to examine regional and global issues related to the live primate trade. Below we explore global patterns of primate trade across regions, species, and purposes using the CITES Trade Database. We included all trade in live primates between 2010 and 2022 as reported by exporting and importing countries (2010–2022 downloaded in March 2024; CITES Trade Database, 2024). We acknowledge that all data from most recent years may not have been reported to CITES yet (see Kolby & Reaser, 2024 for a critical evaluation of CITES data). First, we explored global patterns in trade, then combined data from different countries into three regions: Central and South America (hereafter American tropics including the Caribbean), Africa, and Asia and the Middle East (hereafter Asia). We reported and visualized the proportion of primates traded globally, and for each region, from different sources and for different purposes. We took definitions of source codes and purpose codes directly from the CITES Database Guide (CITES, 2022). We decided not to include any specimens traded because of the difficulties in interpreting the data in the CITES Trade Database; however, the specimens trade also affects

thousands of primates. There may be discrepancies in how management authorities interpret the different purpose and source codes.

From 2010–2022, we found that 142 exporting CITES parties (countries that are signatories to CITES) reported exporting a total of 637,308 live primates. Although 188 species of live primates were traded, *Macaca* were exported in vastly higher quantities than any other genus. *Macaca* exports (569,200 individuals) were 32 times greater than exports of the second-most traded genus:

Callithrix (marmosets; 17,536 individuals).

The three most traded genera were exported at a somewhat stable level over each of the 13 years between 2010–2022 (Supplementary Information ESM 1). However, the less traded genera fluctuated markedly over time and many species showed greater fluctuation between 2020–2022 (Fig. 1).

In general, reported imports and exports differed each year (Fig. 2). However, in 2019–2021, this discrepancy increased and reached an extreme with 57,207 individuals listed as exported but only 17,473 individuals imported in 2021. The SARS-CoV-2 pandemic may have contributed to this trend; however, it is unclear whether this decrease in reported exports and imports truly corresponds to a reduction in trade or simply a delayed report to CITES. Since the beginning of the pandemic, countries like the United States—one of the largest importers of primates for biomedical research—have increased their demand (Subbaraman, 2021). Recent investigations led by media outlets revealed that China's booming biomedical and pharmaceutical industry has contributed to the large-scale illegal trading of

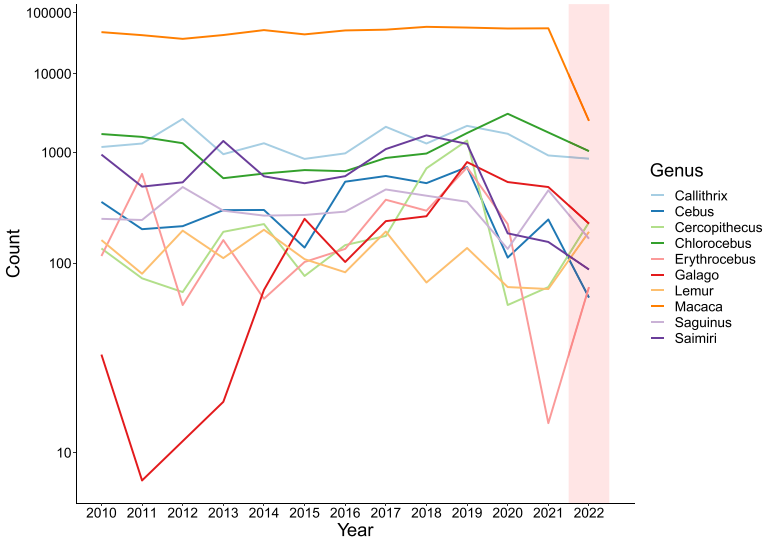

Fig. 1 Overview of the ten most exported live primate genera 2010–2022 globally as reported by the CITES Trade Database (CITES Trade Database, 2024). Counts are presented on a log-scale for figure clarity and comparability among genera. Before log-transforming the data, we added one to all yearly quantities to account for zero values. The year 2022 is highlighted to illustrate potentially incomplete information. The raw numbers of exports for each genus per year can be found in the Supplementary Information (ESM 1).

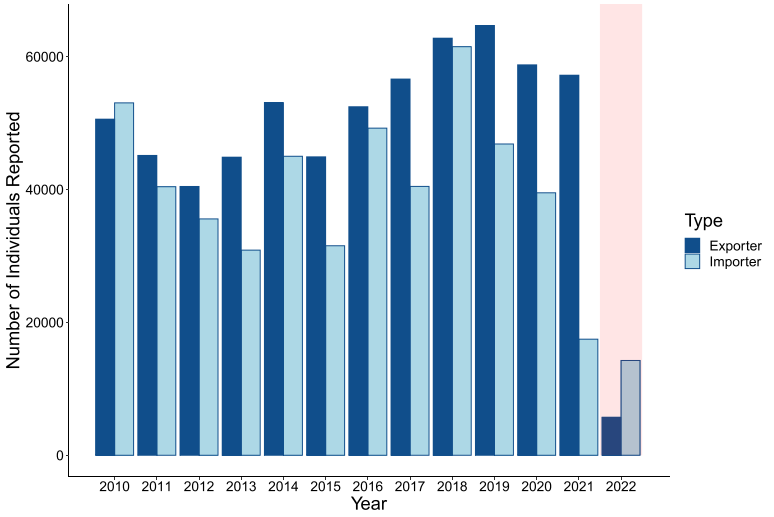

Fig. 2 Total number of primates, of all genera, reported to the CITES Trade Database (CITES Trade database, 2024) as exporter (dark blue bars) and importer (light blue bars) each year across 2010–2022. These data include all live primates reported from all countries, from all sources, and for all purposes. The year 2022 is highlighted to illustrate potentially incomplete information.

wild-caught primates, as legal breeding facilities fail to keep up with the increasing demand (Pasha, 2023). These reports suggest that the reduction in reported trade in 2020–2022 is unlikely to indicate a true reduction in international primate trade. Instead, the discrepancy between the reported imported and exported primates may have resulted from communication breakdowns during the SARS-CoV-2 pandemic, which led to skewed data reporting internationally. Furthermore, when inspecting the import numbers of *Macaca fascicularis* (the most traded species) during the pandemic, there was a change in trade patterns, with more exports coming from range countries instead of China. This is expected to have had a significant effect on free-ranging populations (Hansen *et al*., 2022b; Warne *et al*., 2023). The total U.S. CDC primate import numbers increased by 49% from 21,861 individuals (*Macaca fascicularis* constituted 20,110 ~ 92%) in 2017 to 32,709 individuals (*Macaca fascicularis* constituted 31,522 ~ 96%) in 2022. In 2017, 29% (6,029 individuals) of *Macaca fascicularis* imports originated from Cambodia (CITES Trade Database, 2022). In 2022, it was 62% (19,618 individuals).

Whereas China historically exported many captive-bred primates, they appear to have reduced macaque exports for research in 2019, and some evidence suggests countries that took over exporting macaques (Cambodia, Thailand, Vietnam) were not able to provide the same number of captive-bred individuals, leading to falsified source codes on CITES permits (U.S Attorney's Office, 2022; Warne *et al*., 2023). However, when these data were further interrogated, reports from importing countries still indicate that a substantial number of primates were traded from China (Kolby & Reaser, 2024). The increase in the proportion of wild-caught exports from Asia in 2022 may represent a reaction to reduction (or perceived reduction) of

exports from China; however, it also may be due to backlog of reports from some exporters that have not yet been reported to the CITES Trade Database leading to overall lower numbers in the 2022 export counts (Fig. 2). The CITES Trade Database may underestimate the number of wild-caught primates traded, as the capture and trade in free-ranging primates is illegal in many countries (Covey & McGraw, 2014; Shanee *et al*., 2017; Norconk *et al*., 2020). Breeding centers often rely on wild-caught individuals for the replenishment of their breeding population, which is not necessarily documented by CITES or by primate breeding facilities (Hansen *et al*., 2021).

The total export of live primates in 2010–2022 consisted of the following primary source codes: C – captive-bred (75%, N = 440,263), F – born in captivity (18%, N = 115,333), W – wild-caught (7%, N = 41,270). Captive-bred individuals, in contrast to individuals born in captivity, only include those who were bred in a controlled environment. The number of exported live primates differed markedly between continents. Until 2017, most primates exported from Africa were born in captivity. In 2018, however, the greatest proportion of primates exported from Africa (61%, N = 1,936/3,149) were wild-caught. In 2019, 2020, and 2021, primates exported from Africa were mostly bred in captivity (51%, N = 6,400/12,458; 57%, N = 8,310/14,543; and 49%, N = 8,420/17,241 respectively); however, in 2022 the proportion of wild-caught primates exported from Africa increased again to 54% (N = 1,301/2,425). Before 2022, most primates exported from Asia were bred in captivity; however, in 2022, the largest proportion of primates exported from Asia were wild-caught (46%, N = 528/1,168). Across years the majority of primate exported from the American tropics (mean = 91%) were wild-caught (mean wild-caught exports = 1,199; mean total export = 1,443) (Fig. 3).

The trade purposes of live primates exported in 2010–2022 consisted of the following source codes: M – medical (including biomedical research) (19%, N = 103,080), S – scientific (also including biomedical research) (7%, N = 40,307), T – commercial (70%, N = 438,577), Z – zoo (1%, N = 5,581). Commercial refers mainly to live individuals traded for pharmaceutical research and to a lesser extent legally traded and pets; trophies, primate parts are also included but are not captured in this study as they do not constitute live individuals. Across the 13-year period, while primates exported from Africa were mostly reported as exported for medical purposes, primates exported from Asia were mostly reported as exported for commercial use. There was more variation in the reported purposes of primates exported from the American tropics; however, the leading purposes were still medical and commercial (Fig. 4).

The main primate genera exported out of Africa were *Macaca* and *Callithrix* (together comprising >80% of exports). While some *Macaca* species are native to Africa, the CITES database reported no live exports of *Macaca* species native to Africa from Africa between 2010–2022, the 92,471 *Macaca* exported were *Macaca fascicularis,* which are not native to Africa, and which were exported exclusively from Mauritius. The second most exported genus (*Callithrix*) and three of the other genera (*Saguinus, Saimiri, Cebus*) that make up the ten most exported primates from this continent (Fig. 5a) were also nonnative to Africa. Although it is easy to find local, small *Callithrix* breeders who advertise for the pet trade online, large-scale breeders who could produce more than 15,000 animals over 13 years for

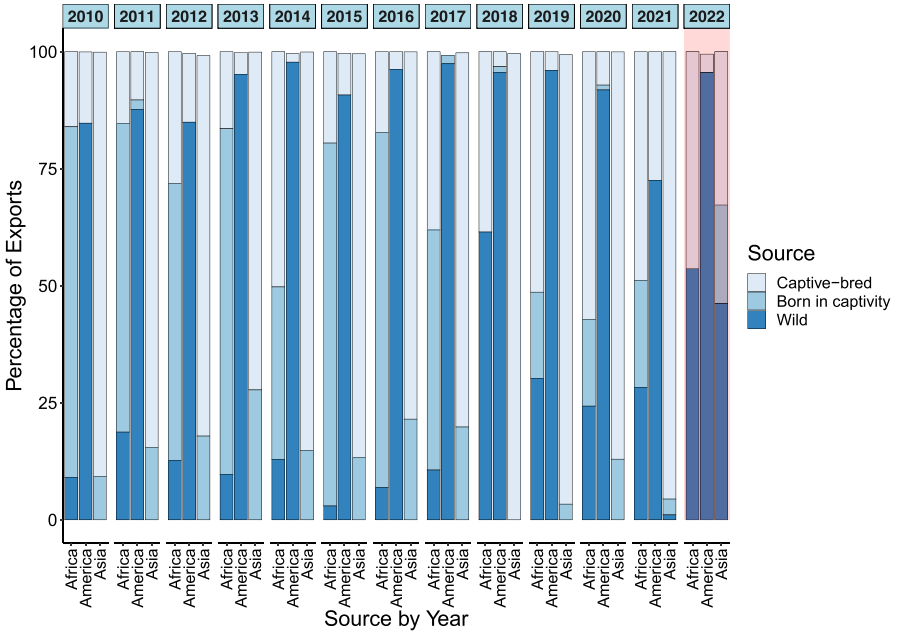

Fig. 3 Proportion of live traded primates from each region (Africa, the American tropics, Asia) from different sources (captive-bred; born in captivity; wild) as reported by the CITES Trade Database (CITES Trade Database, 2024). The year 2022 is highlighted to illustrate potentially incomplete information.

export, are not easily identifiable. Johnson & Anestidou (2019) reported that there were 6,000 *Callithrix* held in research labs in Asia, Europe, North America, and the American tropics. Their review did not document Africa as having or exporting captive *Callithrix*. However, according to the CITES Trade Database, between 2010 and 2022, live *Callithrix* exports were almost exclusively from South Africa (15,561/15,576). The primary driver for the increased yearly demand for common marmosets remains unclear; however, it coincides with *Callithrix* becoming an important biomedical model internationally for research into ageing, infectious diseases, obesity, neurology, heart disease, reproductive biology, cancer, and the microbiome (Johnson & Anestidou, 2019).

The most exported primate genus from Asia was *Macaca,* with more than 400,000 individuals exported over the 13-year period. All other primate genera were traded in much lower quantities, with no other genus having more than 3,000 individual exports reported to CITES over this period (Fig. 5b). Within the genus *Macaca*, *M. fascicularis* were the most exported (N exports = 419,684), followed by rhesus macaques (*M. mulatta*; N exports = 23,285) and pig-tailed macaques (*M. nemestrina*; N exports = 1,783). As of 2022, both *Macaca fascicularis* and *Macaca nemestrina* are listed by the IUCN (International Union for Conservation of Nature) as Endangered (Hansen *et al*., 2022a; Ruppert *et al*., 2022). Finally, *Saimiri* was the most traded genus from the American tropics between 2010–2022 (Fig. 5c). More than 7,700 individuals were exported during this period. *Chlorocebus* (N = 5,314)

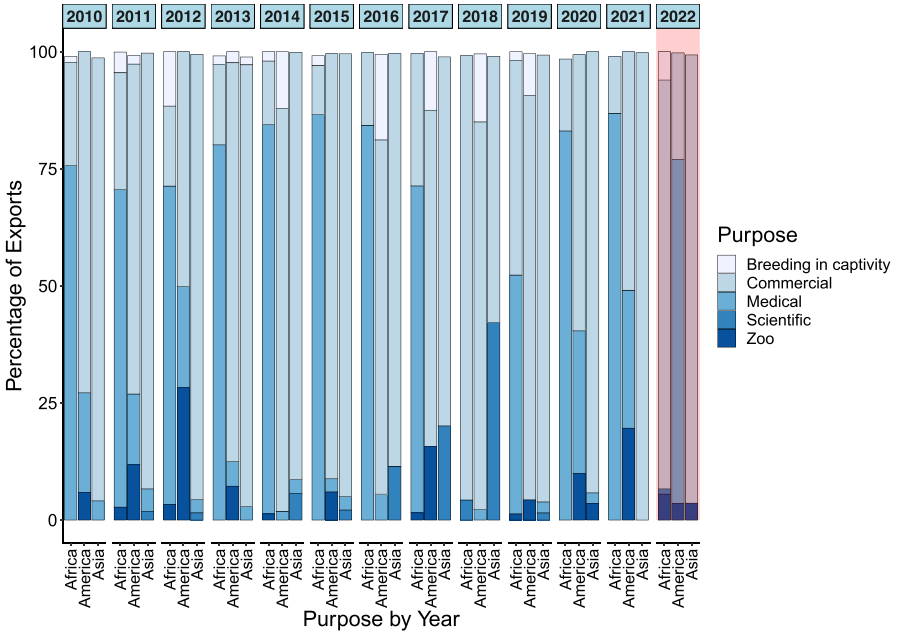

Fig. 4 Proportion of live traded primates from each region (Africa, the American tropics, Asia) for different purposes (breeding in captivity; medical (including biomedical); scientific; commercial (including pharmaceutical); zoo) as reported by the CITES Trade Database (CITES Trade Database, 2024). Only purposes that represented more than 1% of exports in at least one of the regions for at least one of the years are included for figure clarity. The year 2022 is highlighted to illustrate potentially incomplete information.

and *Cebus* (N = 2,418; including *Sapajus*) were the second and third most exported taxa. The genus *Chlorocebus* is not native to the American tropics.

While the most traded primate genera (as reported to CITES) were native to Asia, Africa, and the American tropics, these taxa are often exported out of regions in which they are nonnative (for example, introduced populations on St. Kitts and Mauritius). If individuals are captive-bred, this should not have a marked effect on free-ranging populations. However, the impact on free-ranging populations can vary across geographical regions—for example, wild-caught individuals compose the majority of exports from the American tropics but not Africa and Asia. The high numbers of captive-bred macaques traded may obscure the effects of trade on free-ranging populations of other species from which fewer individuals, but more wild-born individuals, are traded. For example, the proportion of wild-caught primates in the American tropics and in Africa was higher than in Asia from where the majority of captive bred macaques were exported.

These numbers represent the only available internationally regulated trade numbers at the species-level. We do not know the quantity of free-ranging primates killed for the primate meat trade, the quantity of free-ranging primates taken to breeding centres as breeding stock or to supply the international trade,

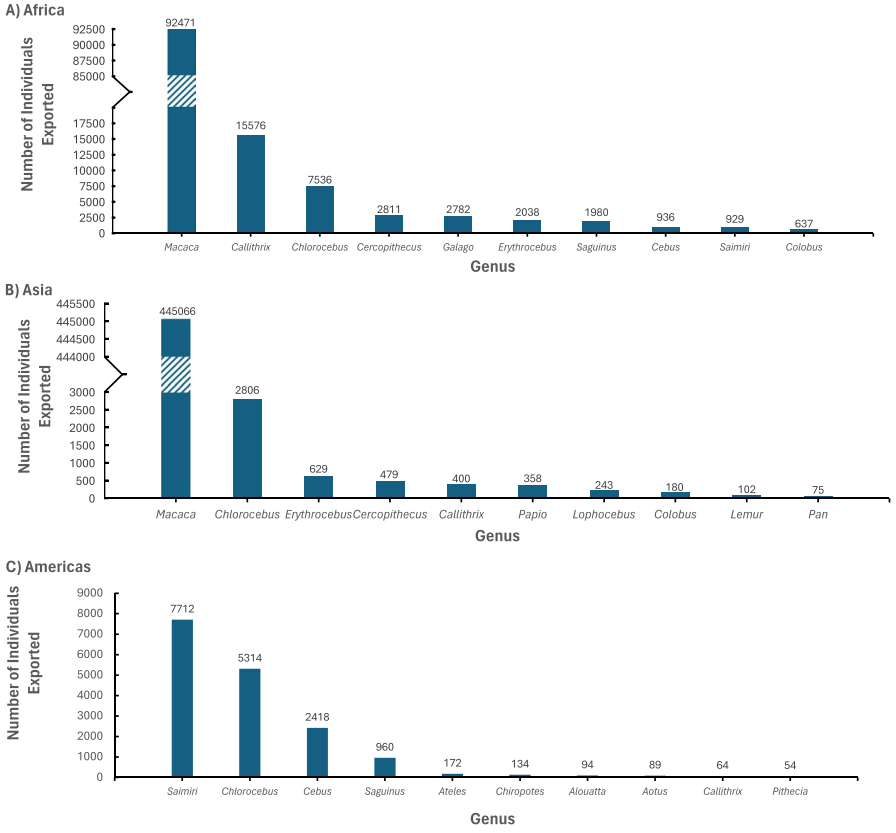

Fig. 5 Top ten exported live primate genera from **A**) African, **B**) Asian, and **C**) the American tropics (including the Caribbean) from 2010–2020 as reported by the CITES Trade Database (CITES Trade Database, 2024). Y-axes are cut between 17,500 and 72.500 individuals in **A** and between 150 and 510,650 in **B** for better visualization as the number of macaques, exported from Asia and Mauritius in Africa were much larger than other genera.

or the quantity captured for the pet and entertainment trades. We do not know the number of wild-caught primates that remain part of the domestic trade and the number traded illegally internationally. Furthermore, the accepted scientific names of several primate species have changed over time, leading to different names being used for the same species or the same names being used for different species. For example, the most common native primate exported from Africa is *Chlorocebus*, commonly named "savanna monkeys," followed by *Cercopithecus*, commonly named "guenon." While these are two different genera of monkeys, changes in classification of these genera may have led to inaccurate reports for the numbers of individuals exported/imported. For example, vervet or savanna monkeys were previously classified as *Cercopithecus*—a name still used today on some websites (African Wildlife Foundation, 2023).

Discussion

We provided an overview of the international live primate trade through five case studies, each highlighting a different area of concern in primate trade. Together they illustrate the importance of combining local and international interventions to minimize the risks that this trade poses to global health and primate conservation. While exporting introduced, potentially invasive, primate populations may not have the same conservation implications as trade in declining natural populations, the risks of disease transmission from transporting and housing primates in close contact with humans remain, as do the welfare concerns with trapping and housing methods. Current methods for safeguarding human populations from the spread of zoonotic diseases from the primate trade are insufficient, with many primates still arriving in importing countries and even exiting quarantine while harbouring infectious diseases. Increased internet access has shifted the way in which primates are traded both locally and internationally, increasing the demand for primate pets. Local NGOs play a critical role in tackling the conservation concerns of trade in wild-caught primate, because they have valuable access to local knowledge and governments. While many primate species are affected by this trade, a few genera—namely *Macaca*, *Callithrix*, and *Chlorocebus*—are disproportionately affected, with regional differences in methods of sourcing animals for the trade and purposes for which they are traded. Lack of transparency and discrepancies in reporting between countries (Kolby & Reaser, 2024; Fig. 2) highlight the need for the inclusion of multiple sources of information when interrogating the primate trade. While these are not an exhaustive list of concerns, they highlight the diversity of issues faced by conservationists and organisations tackling this trade on local and international scales.

Solutions within the primate trade

While suitability for research purposes may be difficult to define, the use of primates for biomedical research and the global trade in primates in general threatens the survival of free-ranging primate populations, and the health of primate ecosystems where the removal of primate species can have detrimental knock-on effects on other species and local human communities (Estrada *et al*., 2017; 2022; Nijman *et al*., 2017; Fernández *et al*., 2022). Furthermore, because of the close phylogenetic relatedness between humans and other primates, the live animal trade also creates conditions in which bidirectional zoonotic disease transmission may occur between humans and other primates, threatening the health of both human and nonhuman populations. We suggest some possible solutions to the issues discussed in this paper.

Given the extreme levels of habitat destruction and fragmentation across their natural ranges, the ever-expanding use of specific species (such as *Callithrix jacchus* and *Macaca fascicularis*) in biomedical research, and the ongoing wild primate population declines, we recommend a moratorium on the capture and trade in wild-caught primates and ask that the biomedical research community work closely

and share resources with the conservation community to protect and restore primate populations and their habitats. We advocate that up to 1–5% of all grants for primate biomedical experimentation be used for conservation for the study species. It is only by growing the free-ranging populations and protecting their natural habitats that we can ensure that primate species will survive past the end of this century (Estrada *et al*., 2017). We encourage improved overall transparency in the trade and in documenting the use of any wild-caught primates for breeding center populations. Furthermore, adopting alternative research methods that do not require the use or trade in wild-caught primates and moving toward methods that minimize or eliminate the use of primates altogether will reduce the health, welfare, and conservation concerns associated with all primate trade.

We recommend that even where removal of primates from free-ranging populations does not lead to substantial population decline in native populations, consideration should still be given to the public health risks associated with primate trade and the welfare of the captured individuals. While removal of introduced, "pest" populations has been seen as a possible solution, the sustainability of these alternatives as "long-term" solutions is unclear. Furthermore, the perceived local overabundance of these introduced populations may skew the global perceptions of the impact the trade has on some globally threatened species. For example, while long-tailed macaques are seen as abundant in Mauritius (Case Study 1), continued trade of wild-caught individuals puts them at risk of extinction in parts of Southeast Asia (Hansen *et al*., 2021). We ask for an international moratorium on the use of wild-caught primates due to immense risks to the species traded, the humans in the trade, and the local ecosystems and communities from where they are removed. We further recommend reading the two recent statements from the International Primatological Society and the IUCN Species Survival Commission Primate Specialist Group, Section on Human-Primate Interactions on the use of wild-caught primates in biomedical and pharmaceutical research (IPS, 2022; IUCN SSC PSG SHPI, 2023).

Outstanding Questions

A major part of the trade in non-human primates is the trade in specimens for pharmaceutical (included under the purpose code T - Commercial) and biomedical (purpose code M - Medical and S - Scientific) use, including blood, tissue, and other body parts. This often results in the extended or permanent removal of individuals from their populations (as described in the 2022 International Primate Society's policy on the capture of free-ranging primates for biomedical research (IPS, 2022)). More than 700,000 *Macaca fascicularis* specimens were traded between 2008–2019 (Hansen *et al*., 2022a, 2022b). The nature of the trade in what is defined as "specimens" is difficult to decipher, and it goes largely unnoticed as most importers order specimens through subcontractors (Hansen personal observation, 2021). Specimens in the CITES Trade Database can be listed in milliliters, liters, grams, pieces etc. It is therefore difficult to know the number of individual primates needed for these specimens. Reporting of exports of noninvasively collected biological samples (e.g., hair, urine, and faeces collected from free-ranging primates) from CITES-listed

species also varies among countries, with some requiring CITES export permits, while others do not, leading to further inconsistencies. In addition, some source and purpose codes provided by CITES are open to interpretation. For example, it is unclear which purpose category best captures the primates traded as pets. Exporters may interpret these codes and categories differently leading to discrepancies between export numbers in the categories when the source and purpose of primates are reported, which may not be a legal question, but it does make it difficult to interpret and understand the trade.

From traumatizing capture and transport methods to barren and/or solidary housing conditions, the welfare of primates in the trade is a concern at every level of the industry (Franklin, 2024). Capturing methods often indiscriminately separate closely bonded individuals and cause high levels of stress and injury; transport involves long (sometimes exceeding 70 hours) periods in which individuals are typically confined in isolation and exposed to a range of fear-inducing stimuli, from loud noises to turbulence. Little knowledge about the needs of each species and lack of national legislation to control housing standards means that many primates are kept in inadequate husbandry standards (Prescott & Jennings, 2004). Indeed, one report found that more than 28% of *Nycticebus coucang* (greater slow loris, including all infants) confiscated from illegal trade routes died within 6 months, mostly from traumatic injuries (Fuller *et al*., 2018). More than 25% of survivors also exhibited abnormal behavior associated with heightened stress or trauma (Fuller *et al*., 2018). While a thorough discussion of the welfare implications of the primate trade was beyond the scope of this paper, the welfare and wellbeing of primates within the primate trade is a major concern that should be taken into consideration for policy making.

Conclusions

Our case studies show that some primate populations (such as those introduced to islands) are disproportionately affected by the global primate trade and highlight risks of disease transmission, implications from the rise of online markets, and the need for conservation strategies to be tailored to each region and species. While the exports reported to CITES are primarily of captive-bred individuals, individuals are more likely to be reported as "wild-caught" when traded out of the American tropics and Africa (e.g., from introduced island populations). These reports are likely an underestimate of the true number of wild-caught primates traded, because it often is illegal to capture free-ranging primates in their range counties (Covey & McGraw, 2014; Shanee *et al*., 2017). Furthermore, in some countries, primates are caught illegally and traded under counterfeit certificates as captive-bred (Pasha, 2023; Weston, 2023; The Nation Thailand, 2023; Warne *et al*., 2023). The case studies addressed in this paper did not consider the unknown numbers of primates traded domestically. While these numbers are difficult to track, domestic trade also threatens free-ranging populations and often is unregulated (Hicks *et al*., 2010; Hansen *et al*., 2021). Given the impending primate extinction crisis (Estrada *et al*., 2017, 2022), efforts should be made to monitor and combat this trade where it endangers wild primates. Nevertheless, large-scale, international strategies may

be required to tackle the growing online trade and the attendant risk of disease transmission, as part of the One Health approach.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10764-024-00431-9.

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Author contributions PAG, FD, SL, MFH, and VN conceived and designed the concept. MG downloaded the data and sorted it. DRKN, VN, and GB analysed and visualised the data. All authors contributed to the writing and reviewing of the manuscript.

Declarations

Ethical Statement All data used for this paper were gathered from existing online datasets. This research and data collection adheres to the *American Journal of Primatology's* Principles for the Ethical Treatment of Non-Human Primates. We declare no conflicts of interests for any co-authors of this manuscript.

Data availability The data that support the findings of this study are available in CITES Trade Database at https://trade.cites.org/. These data were derived from the following resources available in the public domain: CITES Trade Database; https://trade.cites.org/. Reformatted data used to generate figures are available in the following GIThub repository: https://github.com/GalB96/Perspectives-on-the-Global-Primate-Trade.

Inclusion and Diversity Statement The author list includes contributors from the location where parts of the research was conducted, who participated in study conception, study design, data collection, analysis, and/or interpretation of the findings.

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