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Review

Preventative Vaccination of Nonhuman Primates

Remco A. Nederlof [1,*], Sanna Sainmaa [2], Nathalie Wissink-Argilaga [3], Bon-Sang Koo [4,5] and Jaco Bakker [6]

[1] Independent Researcher, 2861 XZ Bergambacht, The Netherlands
[2] Korkeasaari Zoo, 00570 Helsinki, Finland; sanna.sainmaa@korkeasaari.fi
[3] Chipping Norton Veterinary Hospital, Chipping Norton OX7 5SY, UK; nat.wissink@chippingnortonvets.co.uk
[4] National Primate Research Center, Korea Research Institute of Bioscience and Biotechnology, Cheongju 28116, Republic of Korea; porco9@kribb.re.kr
[5] Department of Biomolecular Science, KRIBB School of Bioscience, University of Science & Technology, Daejeon 34141, Republic of Korea
[6] Animal Science Department, Biomedical Primate Research Centre, Lange Kleiweg 161, 2288 GJ Rijswijk, The Netherlands; bakker@bprc.nl
* Correspondence: remco.a.nederlof@gmail.com

Abstract: Vaccination constitutes one of the most important means of preventing infectious disease in captive nonhuman primates (NHPs). Vaccination protocols for NHPs vary, as they are mostly guided by institutional preference, infection pressure, local availability, and recommendations by non-peer reviewed resources. Currently, no updated literature review about vaccination options for NHP is available. Therefore, we provide a detailed overview of published vaccination options for NHP. Our findings demonstrate that, while there are often insufficient scientific data to justify their use, the core vaccines used in most NHP species confer protection against tetanus, rabies, and measles. Where information is available, efficacy expectations, adverse effects, dosages and frequency of administration are provided. We advocate that the decision to vaccinate NHP for less common diseases, for which an off-label vaccine is available, should be grounded in a comprehensive risk assessment. This assessment should consider factors specific to the individual animal, the vaccine, the housing institution, the epidemiology of the disease, and relevant regulatory and ethical considerations.

Keywords: vaccination; NHP; immunization; protocol; recommendations; rabies; tetanus; measles; zoonosis; one health

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1. Introduction

Due to the close phylogenetic relationship between humans and nonhuman primates (NHPs), many infectious diseases are shared between the species. Therefore, the close proximity of captive NHPs in research centers and zoological institutions, as well as urbanized wild NHPs, to humans poses a risk of zoonotic and reverse zoonotic disease transmission [1]. Effective vaccination strategies in NHP populations are therefore critical for disease prevention and control, safeguarding both public and animal health.

While the significance of proper vaccination practices is widely accepted among veterinarians and zoological institutions, the protocols employed are often not grounded in peer-reviewed evidence and may not be suitable for the specific conditions of a particular institution. Consequently, there is considerable variability in vaccination protocols, and inappropriate protocols may result in unnecessary handling of animals, adverse health effects, or the unexpected occurrence of infectious diseases.

This paper aimed to not only address the paucity of the literature surrounding the efficacy and use of vaccines in NHPs, but also to provide veterinary clinicians working

with NHPs with a complete overview of current peer-reviewed evidence on the different vaccines that they may consider in constructing institution-specific immunization protocols. To identify all the relevant literature, we conducted a search for books, book chapters, peer-reviewed publications, conference abstracts, and newsletters in academic literature databases, including PubMed and Google Scholar. The literature pertaining to experimental vaccination of NHPs for human vaccine development was largely omitted. Although experimental vaccines have successfully been used to confer protection against, e.g., West Nile virus [2], Lyme disease [3], Lassa fever [4], and anthrax [5–8], these vaccines are generally not commercially available, and their use may only be considered under exceptional circumstances, e.g., in high-risk populations or during epizootics. Moreover, the use of vaccines in NHPs is considered "off-label", and local regulations should be checked before the use of these vaccines. Where possible, brand-specific information is mentioned. In other instances, however, vaccines are referred to by their formulation.

2. Current Vaccination Recommendations

Large variations exist regarding recommendations and current practices for the immunization of NHPs in different institutions. For example, according to a survey conducted by the European Association of Zoos and Aquaria (EAZA), the majority of the EAZA zoos (79%, 31/39) never vaccinate their capuchin monkeys (*Cebus* sp. or *Sapajus* sp.) Of responding zoos, 15% (6/31) vaccinated against *Yersinia pseudotuberculosis*, 3% (1/31) against rabies, and 3% (1/31) against cowpox [2]. This demonstrates the large variability of vaccination practices, even in similar institutions. Some guidelines have been constructed pertaining to specific species or groups, such as EAZA best practice guidelines (BPGs), EAZA taxonomic advisory group (TAG) recommendations, and Association of Zoos and Aquaria (AZA) care manuals (Table 1). However, there is scarce information in the literature about the efficacy of vaccines in different NHP species, and current vaccination recommendations are often not based on literature but extrapolated from human vaccination regimes and empirical evidence.

Table 1. Current recommendations on the vaccination of NHP in EAZA best practice guidelines and AZA care manuals.

Species	Tetanus	Rabies	Measles	Measles, Mumps, Rubella (MMR)	Poliomyelitis	Influenza	Pneumococcosis	*Haemophilus influenzae*	*Yersinia pseudotuberculosis*	Cowpox	Yellow Fever	Note	Reference
Callitrichidae	(X)	(X)	(X)						X			Measles only when there is a killed vaccine available; no attenuated vaccines of any kind; rabies only when in an endemic area with possibility of contact with wildlife; tetanus only when there is outdoor access.	[9]
Capuchin Monkey (*Sapajus* sp. and *Cebus* sp.)	X	(X)	X						(X)	(X)	(X)	BPG does not provide recommendations but instead reports usage in European zoos; rabies only when in an endemic area with possibility of contact with wildlife; yellow fever vaccination only in endemic areas.	[10]
De Brazza Monkey (*Cercopithecus neglectus*)	X	X										Necessity dictated by risk assessment and official guidelines.	[11]
Colobus monkey (*Colobus* sp.)	X	(X)	X									Rabies only when in an endemic area with possibility of contact with wildlife.	[12]
Gelada baboon (*Theropithecus gelada*)	X											Necessity dictated by risk assessment and official guidelines.	[13]
Mangabey (*Cercocebus* sp., *Lophocebus* sp., *Rungwecebus* sp.)	X	X										Necessity dictated by risk assessment and official guidelines.	[14]
Hamadryas baboon (*Papio hamadryas*)	X	(X)	X									Rabies only when in an endemic area with possibility of contact with wildlife.	[15]

Table 1. *Cont.*

Species	Tetanus	Rabies	Measles	Measles, Mumps, Rubella (MMR)	Poliomyelitis	Influenza	Pneumococcosis	*Haemophilus influenzae*	*Yersinia pseudotuberculosis*	Cowpox	Yellow Fever	Note	Reference
Western Lowland Gorilla (*Gorilla gorilla gorilla*)	X	(X)	(X)	(X)	X	X						Rabies only when in an endemic area with possibility of contact with wildlife; measles vaccination is recommended, either as stand-alone or as part of the MMR vaccination.	[16]
Western Lowland Gorilla (*Gorilla gorilla gorilla*)	(X)	(X)		(X)		(X)						Routine vaccination of great apes is generally not recommended; tetanus not currently a reported issue in European gorillas.	[17]
Western Lowland Gorilla (*Gorilla gorilla gorilla*)	X	(X)	X		(X)	X		(X)				Rabies only when in an endemic area with possibility of contact with wildlife; polio is considered to be optional; *Haemophilus* is considered to be optional.	[18]
Chimpanzee (*Pan troglodytes*)	X	(X)	(X)	(X)	X	X						Rabies only when in an endemic area with possibility of contact with wildlife; measles vaccination is recommended, either as stand-alone or as part of the MMR vaccination.	[16]
Chimpanzee (*Pan troglodytes*)	X		X		X								[19]
Bonobo (*Pan paniscus*)	X	(X)	(X)	(X)	X	X						Rabies only when in an endemic area with possibility of contact with wildlife; measles vaccination is recommended, either as stand-alone or as part of the MMR vaccination.	[16]
Chimpanzee (*Pan troglodytes*)	X	(X)	X		X							Rabies only when in an endemic area with possibility of contact with wildlife.	[20]
Orangutan (*Pongo* sp.)	(X)		X		(X)							Tetanus and poliomyelitis vaccines have yet to be reported, and are currently not recommended.	[21]
Orangutan (*Pongo* sp.)	X	(X)	(X)	(X)	X	X	X					Rabies only when in an endemic area with possibility of contact with wildlife; measles vaccination is recommended, either as stand-alone or as part of the MMR vaccination.	[16]
Orangutan (*Pongo* sp.)	X	(X)				X	X	X					[22]
Slow loris (*Nycticebus* sp.)	X	X										No information exists on the efficacy of the vaccines or the inclination to develop disease.	[23]
Sifaka (*Propithecus* sp.)		(X)										Killed rabies vaccine is possible when in an endemic area with possibility of contact with wildlife.	[24]

Recommendations marked by 'X' are advised at all times. Recommendations marked by '(X)' are only advised under specific circumstances.

Currently, no universal evidence-based recommendation for immunization in NHPs exists. In fact, a one-size-fits-all approach may not be desirable, as the decision to vaccinate NHPs may depend on a range of factors (Table 2). The considerations presented in Table 2 are based on literature, personal experience, and empirical information. These considerations can be used as a starting point for veterinary clinicians when constructing a vaccine protocol for NHPs.

Table 2. Factors to consider when designing a vaccination protocol for zoological institutions.

Animal Considerations	Vaccine Considerations	Regulatory and Ethical Considerations	Institutional Considerations	Epidemiological Considerations
• Species; • Age; • Current and past health status; • Vaccination status and history.	• Efficacy; • Safety; • Adverse effects; • Necessity for booster immunizations; • Cost; • Product availability; • Storage requirements.	• Health and welfare risks associated with procedures surrounding the vaccination; • Compliance with local legal guidelines surrounding off-label administration of vaccines to NHPs.	• Enclosure design and evaluation of exposure risk to and of staff, public, or other disease vectors; • Frequency of routine hands-on medical evaluation; • Training of animals for body part presentation and intramuscular (IM) injection; • Biosecurity protocols for primate staff; • Interference with biomedical research in research facilities; • Staff training and expertise; • Disease surveillance.	• Infectious disease prevalence and incidence in both the human and NHP populations in the geographic area; • Route of transmission; • Expected severity of disease; • Zoonotic risk.

3. Available Vaccines

Nowadays, morbidity and mortality associated with a wide range of infectious agents may be reduced or prevented due to a diverse array of vaccines that have been developed. Vaccine types include live (attenuated), killed (inactivated), subunit, recombinant, conjugate, toxoid, DNA, mRNA, viral vector, recombinant vector, whole-cell, and nanoparticle

vaccines [25]. If possible, live vaccines that have not been evaluated in a given NHP species should be avoided, as there is an unknown risk of return to virulence when administered to non-target species. Due to the geographic and institutional variations in incidence of specific pathogens, no attempt has been made to organize the following paragraphs based on relevance. Instead, the following paragraphs are grouped based on the type of pathogen and subsequently organized alphabetically.

4. Bacterial Pathogens

4.1. Bacterial Meningitis

Streptococcus pneumoniae is a Gram-positive bacterium and a common inhabitant of the human respiratory tract. It is recognized as an important cause of pneumonia in great apes, particularly following previous viral infection [26–28]. *Haemophilus influenzae* is a Gram-negative bacterium that similarly is commensally present in the nasopharynx of most humans. Both *S. pneumoniae* and *H. influenzae* have been reported as causative agents for bacterial meningitis in NHPs [29–32]. According to the great ape TAG, juvenile and geriatric bonobos and orangutans are particularly susceptible to pneumococcosis, that is, *S. pneumonia* infection [16].

Human vaccines are available for both *H. influenzae* and *S. pneumoniae*, but little research has been conducted into their effectivity in NHPs.

The *H. influenzae* vaccine is a conjugate vaccine designed for IM administration in humans. No peer-reviewed literature exists on its use in NHPs, and as a result, no information is available on its safety and efficacy profile in NHPs.

Both conjugate and polysaccharide *S. pneumoniae* vaccines exist. One report suggests that IM vaccination against *S. pneumoniae* using a conjugate vaccine was unsuccessful in a group of chimpanzees [30]. No other peer-reviewed reports are available on the use of either conjugate or polysaccharide *S. pneumoniae* vaccines in NHPs.

Despite this paucity of information, the AZA care guide recommends vaccination against both *H. influenzae* type B and *S. pneumoniae* in juvenile orangutans [22]. Juveniles at high risk may be vaccinated at the age of 2, 4 and 6 months with the children *S. pneumoniae* vaccine containing 13 serovars, followed by the adult vaccine containing 23 serovars at the age of 18 months, subsequently boostered every 10 years [16].

4.2. Klebsiella pneumoniae

Klebsiella pneumoniae is a Gram-negative, non-spore-forming, facultative anaerobic, rod- to coccobacillus-shaped, encapsulated bacterium. Infections result in significant morbidity and mortality in NHPs and are associated with peritonitis, septicemia, air sac infection, pneumonia, diarrhea, and meningitis in both Old World (OW) and New World (NW) primate species [33–36].

Vaccination with a killed, whole *K. pneumoniae* aluminum hydroxide-adsorbed bacterin vaccine in gray-bellied night monkeys (*Aotus lemurinus*) and a capsular polysaccharide vaccine in squirrel monkeys (*Saimiri* sp.) has been effective in reducing morbidity and mortality in the respective colonies [37,38]. Autogenous vaccination has also been used in a breeding colony of common marmosets (*Callithrix jacchus*) [39]. In a study involving night monkeys, both infants and adults were vaccinated with two 0.5 mL doses of formalin PBS 1:10 diluted bacterin without adjuvant administered SC at one-month intervals. A seroconversion rate of 90% was reported after the second dose, and mortality due to *K. pneumoniae* infections dropped from 20–22% to 3–4% following vaccination. However, drawbacks included the development of small granulomas (0.5–1 cm) with fistulous tracts at the inoculation site and the death of two night monkey infants less than one month old from bacterin-associated endotoxemia [37]. Similarly, the capsular polysaccharide vaccine

was successful in the squirrel monkey colony. In this study, 50 µg capsular polysaccharide in 0.1 mL 0.9% NaCl was administered once subcutaneously. The vaccine was successful in reducing the total infant mortality from 45 to 20%, but without any observed adverse effects [38].

Although these studies demonstrate the efficacy and safety profiles of different vaccines in reducing *K. pneumoniae*-associated morbidity and mortality, *K. pneumoniae* vaccines are not widely available. Furthermore, the safety profiles for most NHPs remain largely unknown. The death of two infant night monkeys suggests that even inactivated *K. pneumoniae* vaccines may not be appropriate for all animals. Yet, the effectiveness in lowering mortality rates in night and squirrel monkeys highlights the potential of these vaccines.

4.3. Leptospirosis

Leptospirosis is a zoonotic disease caused by bacteria of the genus *Leptospira* [40]. Currently, 66 pathogenic and non-pathogenic *Leptospira* species are recognized, including over 300 different leptospiral serovars [40–42]. Rodents constitute the natural reservoir for a multitude of *Leptospira* serovars [43,44]. Outbreaks of leptospirosis have been reported in both free-ranging and institutionally kept OW and NW NHPs around the world [45–51]. Clinical symptoms reported in NHPs include lethargy, anorexia, diarrhea, vomiting, jaundice, and death [46,47].

Elimination of leptospiral infection from a squirrel monkey population was accomplished by immunization with a formaldehyde-inactivated vaccine containing 2×10^8 cells/mL of *L. interrogans* serovar *copenhageni*. Monkeys were vaccinated SC with two 1 mL doses administered three weeks apart. No adverse effects were reported [52]. No reports exist on the use of similar vaccine preparations in other NHP species.

A paucity of information exists on vaccination against leptospirosis in NHPs. Although little information exists on the efficacy of commercial canine leptospirosis vaccines in NHPs, they may still be considered to reduce clinical disease in NHPs considered to be at risk [53]. One must bear in mind that safety and efficacy profiles are unavailable for canine leptospirosis vaccines, and that preventative measures, such as pest control plans, may constitute a more practical approach to reducing leptospiral morbidity and mortality.

4.4. Tetanus

Clostridium tetani is a Gram-positive, spore-forming, obligate anaerobic rod that is ubiquitously present in the soil and digestive tracts of animals and humans [54]. Inoculation of a wound with *C. tetani* spores may allow for germination with subsequent production of tetanospasmin. This neurotoxin induces the clinical signs, which are predominated by hyperactivity of voluntary muscles leading to rigidity and tetanic spasms [54]. Tetanus has been reported to cause morbidity and mortality in a wide range of NHP species, and it may affect any species [55–57]. Fatality rates are reportedly as high as 77–100% in NHPs [55,58]. Prior to vaccination, tetanus-associated deaths have been reported to account for 24.7% of all deaths in a tropical colony of rhesus macaques (*Macaca mulatta*) [59]. Despite causing high mortality rates, tetanus is not currently reported in NHPs in Europe, and many animals are reported to be unvaccinated for this disease [17].

Commercial tetanus vaccines utilize tetanus toxoid to induce protective immunity against *C. tetani* neurotoxin. One study reports that an immunization program consisting of two intramuscular doses of tetanus toxoid provided long-term, likely lifelong protection against tetanus in a colony of rhesus macaques, and completely reduced the colony mortality rate due to tetanus infection to 0% [55]. Moreover, it has been reported that Super-Tet® with Havlogen® (Intervet/Merial, Whitehouse Station, NJ, USA), another tetanus toxoid vaccine, induced the highest levels of tetanus antitoxin in macaques when both were ad-

ministered at 0.5 mL IM simultaneously, boostered after one year. Although the duration of immunity is unknown, the observed titers are expected to confer protective immunity for at least five years based on human studies. No adverse effects were observed following vaccination with either vaccine [55]. Also, the long-term effects of vaccination were demonstrated in free-ranging rhesus monkeys, including improved health and well-being, increased survivorship, enhanced reproductive value, and extended life expectancy [60]. A wide variety of tetanus toxoid products are currently marketed that may be used to vaccinate NHPs.

Many recommendations exist on the dosage and frequency of administration in different NHP species. Some literature exists describing vaccination intervals in marmosets and macaques. Vaccination with IM tetanus toxoid has been described in common marmosets at 0 months, with boosters at 3 months and 12 months [61]. Boosters are advised at intervals of between 5 and 10 years by the callitrichid BPG [9]. In macaques, it is reported that two 0.5 mL doses of tetanus toxoid administered IM at one-year intervals confers immunity that may last up to 18 years [55]. A study conducted in rhesus macaques demonstrated that annual vaccination results in seropositivity rates of 65%, 93%, and 100% following the first, second, and third vaccinations, respectively. Protective antibody titers were reported in all age groups, but significantly higher antibody titers were observed in juvenile animals compared to adults and elderly individuals. Moreover, this article proposes a vaccination schedule consisting of two annual doses followed by a booster immunization every five years [62]. Free-ranging rhesus macaques that received a primary vaccination at one year of age and a booster vaccination at two years of age demonstrated complete and lifelong immunity against tetanus infection [60].

Different guidelines propose vaccination schedules for species for which no further literature is available. The capuchin BPG recommends two primary IM injections of 0.5 mL each, at intervals of 4–5 weeks and a booster 6–12 months later. This booster may be repeated at a frequency between 1 and 10 years [10]. The AZA care manuals for the Colobus monkey (*Colobus* sp.) and hamadryas baboon (*Papio hamadryas*) both propose three protocols: 0.5 mL IM at 5–7 and 13–15 months of age, then booster every 5 years with 1 mL; 0.5 mL IM at 3, 6, and 9 months of age, then booster every 3–5 years with 1 mL; or 1 mL IM at 2, 4, 6, and 18 months of age, then booster every 5–10 years [12,15]. In chimpanzees (*Pan troglodytes*), three IM doses of tetanus vaccine are given at 2–3-month intervals, starting at 3 months of age. A booster is given after 5 years, and at 10-year intervals thereafter [19]. Similar recommendations exist for Western lowland gorillas (*Gorilla gorilla gorilla*) and orangutans (*Pongo* sp.). For these species, three standard human doses of tetanus vaccine IM should be administered. The first dose may be given from 4 months old. The second dose should be given 4–8 weeks after the first dose. A third dose should be given 6–12 months after the second dose, then booster at 5–10-year intervals [16,17].

It has also been proposed that the vaccine dose should be adjusted for the smaller size of NW and OW NHPs to reduce adverse injection-site effects. Proposed dosages are 0.05–0.1 mL for callitrichids, 0.25 mL for medium-sized primates, and 0.5 mL for larger primates [63]. No efficacy studies have been conducted in most species, nor have any been performed with reduced dosages, and these recommendations should be cautiously interpreted until efficacy studies become available.

Although no reports exist, there is a general feeling among primate experts that human combined vaccine preparations against diphtheria, tetanus, and pertussis (DTP) should not be administered, as they may produce serious, potentially fatal side effects [64].

Tetanus vaccines are affordable in most countries, appear to be safe in all NHPs, and are reportedly effective in reducing tetanus-associated morbidity and mortality in macaques [55,62]. Many institutions do not routinely vaccinate their NHPs, and tetanus

is rarely reported in some areas. Nevertheless, the ubiquitous nature of *C. tetani* and the significant morbidity and mortality the agent may cause advocate for the use of tetanus toxoid vaccines in NHPs, particularly in animals with outdoor access [9].

4.5. Yersinia pseudotuberculosis

Yersinia pseudotuberculosis is a Gram-negative, aerobic, pleomorphic coccobacillus. The bacterium is zoonotic and the causative agent of clinical yersiniosis [65]. The bacterium is transmitted via the fecal–oral route from a reservoir in wild rodents and birds [66–69]. Outbreaks of yersiniosis have been reported in a wide range of both mammalian and avian species, including brown-headed spider monkeys (*Ateles fuscisceps*), squirrel monkeys, and silvery marmosets (*Mico argentatus*) (recently reviewed in [70]). Reported clinical symptoms in NHPs include anorexia, apathy, diarrhea, ataxia, and sudden death [69,71,72].

In the past, a formol-killed vaccine adsorbed onto aluminum hydroxide gel has been administered to colonies of silvery marmosets (*Callithrix argentata argentata*), white-headed marmosets (*Callithrix geoffroyi*), and goeldi's marmosets (*Callimico goeldii*). The vaccine contained a titer of approximately 1.04×10^{11} CFU/mL and failed to provide significant protection when administered intramuscularly twice with 30 days interval followed by an annual booster vaccination. No adverse effects were observed following administration of this vaccine [73]. Further research may reveal the underlying mechanisms for a lack of vaccine efficacy in marmosets. Until these are discovered and addressed, it is recommended to use commercial vaccines instead.

Two commercial vaccines are available. Pseudovac® (Utrecht Veterinary Faculty, Utrecht, The Netherlands), a killed whole-cell vaccine composed of serotype 1 to 6 isolates, is commercially available in Europe [74]. Another vaccine, Yersiniavax® (MSD Animal Health, Upper Hutt, New Zealand), contains inactivated *Y. pseudotuberculosis* serotypes 1 to 3, and is commercially available for deer. Unfortunately, no literature exists evaluating either vaccine in NHPs, and as a result, no information on vaccine efficacy or safety profile is available for these species.

Immunization against *Y. pseudotuberculosis* is recommended by the capuchin BPG at a dose of 0.5 mL SC in animals older than seven weeks, with a booster 3–6 weeks later. Booster immunizations may be administered annually [10].

Identification of risk factors associated with yersiniosis is crucial due to the difficulty associated with its treatment, as well as the apparent inefficacy of the available vaccines. Nevertheless, an emergency booster vaccination in case of an epizootic event may be considered as an alternative to metaphylactic antibiotic treatment for animals without clinical signs of disease [70].

5. Viral Pathogens

5.1. Ebola Viruses

Orthoebolavirus is a genus within the family *Filoviridae* and encompasses six species. The members of this genus are named after the region in which they were originally identified: Bundibugyo virus (BDBV), Reston virus (RESTV), Sudan virus (SUDV), Taï Forest virus (TAFV; formerly Côte d'Ivoire ebolavirus), ebolavirus (EBOV), and Bombali virus (BOMV). Of these ebola viruses, EBOV and TAFV have been reported in wild great apes [75,76]. The exact reservoir range of ebolaviruses is unknown, but bats of the *Pteropodidae* family are considered to be natural reservoirs [77]. Ebola virus disease (EVD) may be transmitted through direct contact, contact with bodily fluids, or contact with deceased animals. EVD is rarely observed in wild apes, but reported symptoms include lethargy, hyporexia, abdominal pain, vomiting, diarrhea, and internal and external hemorrhages [75,78]. Total population mortality associated with TAFV has been estimated around 25% during

one outbreak in chimpanzees, with an approximated near 100% case fatality rate [75]. In areas where EBOV outbreaks occurred, population declines of 90% in gorillas and 98% in chimpanzees have been reported [79].

In general, non-neutralizing antibodies are considered to be primarily responsible for humoral protection against filovirus infections [80,81]. Various experimental and commercial vaccines have been investigated, and two vaccines are currently licensed.

ERVEBO® (Merck, Kenilworth, NJ, USA), or rVSV-EBOV, is a live attenuated recombinant vesicular stomatitis virus vector-based vaccine that expresses the transmembrane glycoprotein (GP) of EBOV. This vaccine has been demonstrated to confer protection against EBOV, but not SEBOV, challenge when administered as a single 10^7 PFU dose IM in cynomolgus macaques [82]. Moreover, a follow-up study demonstrated that intranasal and oral administration of 2 mL of 10^7 PFU/mL vaccine similarly conferred protection against disease in all cynomolgus macaques when challenged 28 days after immunization. Intranasal administration resulted in IgG titers 8–9-fold higher than in oral and IM routes. Both intranasal and oral routes induced high IgA titers [80]. No adverse effects have been reported in macaques following administration [80,82]. The downsides of this vaccine include the necessity for cold chain storage at −70 °C or lower, and reported adverse effects in humans, including transient arthritis and pyrexia [83,84].

The other licensed vaccine, Zabdeno/Mvabea® (Janssen, Pharmaceutical Companies of Johnson & Johnson, New Brunswick, NJ, USA), consists of two different compounds. The first, Zabdeno®, is a replication-deficient adenovirus type 26 vector-based vaccine expressing EBOV GP. The second, Mvabea®, is an MVA vector-based vaccine encoding GPs from EBOV, SUDV, Marburg virus, and a nucleoprotein from TAFV. These doses, both 0.5 mL administered IM, are recommended to be administered eight weeks apart in humans. In cynomolgus macaques, this prime-boost vaccination regimen conferred full protection against challenge with 100 PFU of the EBOV Kikwit strain without observed adverse effects [85].

Research into novel vaccines is ongoing, as current parenteral administration routes may be inappropriate for mass immunization of wild great ape populations. A rhesus cytomegalovirus (RhCMV) vector-based vaccine has been developed specifically for wild great apes, and it is able to spread between individuals. The vaccination protocol consisted of the SC injection of 1×10^7 PFU at Days 0 and 28. This vaccine protected 80% (5/6) of rhesus macaques against lethal EBOV challenge. One animal developed mild signs of disease but survived. Survival appeared to be correlated with EBOV GP-specific IgG, as the single animal that died demonstrated the lowest IgG titers [86].

In chimpanzees, trials have been performed with filorab1, which is a replication competent, highly attenuated SAD B19-based rabies virus vaccine encoding the EBOV GP. The single administration of 1.5×10^8 focus forming units of vaccine in six chimpanzees resulted in similar immune responses when administered orally or intramuscularly. No adverse effects were observed. The reported immune responses were comparable to those observed in an EBOV vaccine trial using a virus-like particle (VLP) vaccine [87,88]. No virus challenge has been performed following vaccination in chimpanzees, and, as a result, no statements can be made on vaccine efficacy.

A VLP-based vaccine has been used in captive chimpanzees. This vaccine does not replicate and is considered to be safe in both chimpanzees and macaques [88,89]. Although no challenge was performed in chimpanzees, strong IgG responses were observed that were protective in mice in a passive transfer efficacy study. This trial used three IM immunizations of 3 mg of VLPs with 25 mg of either IDC-1001 or CpG ISS 1818 on Days 0, 29, and 56. The necessity for multiple parenteral administrations may pose logistical challenges for its use in wild populations [88]. Moreover, a novel VLP vaccine has been

developed, but is still in the experimental phase. This bivalent vaccine incorporates EBOV and SUDV GPs on a spherical HIV-1 Gag core. This vaccine induces robust cellular and humoral responses in rhesus macaques when administered IM on Days 0 and 28. Moreover, this vaccine elicits antibodies that are not only reactive to EBOV and SUDV GPs, but also cross-reactive against BDBV GPs.

The currently available vaccines may induce long-term protection, although the exact duration is unknown. As a result, these vaccines may be used in captive great apes that are at risk of EVD.

However, for use in at-risk wild great apes, additional considerations must be taken into account. For example, the unknown duration of protection, be it months or a few years, may not be sufficient to prevent EVD epizootics in wild populations long-term [90]. Moreover, a major drawback of both licensed vaccines is the necessity of administering them to individual animals. Immunization of non-habituated wild great ape populations may impose significant logistical difficulties. The reported oral administration routes in ERVEBO® and filorab1 offer the possibility of baited vaccines, which may be used in wild populations. Nevertheless, great apes are selective eaters, and it may prove difficult to ensure that all intended individuals receive adequate doses of the vaccine. Alternatively, self-spreading vaccines, such as the RhCMV vector-based vaccine, may constitute a more viable approach of immunizing wild populations. However, before such vaccines can be applied, thorough research is warranted into their safety and efficacy in great apes. Moreover, regulatory and ethical considerations must be taken into account before proceeding with the vaccination of wild NHPs.

5.2. Encephalomyocarditis (EMCV)

The encephalomyocarditis virus (EMCV) belongs to the genus *Cardiovirus A* within the family *Picornaviridae* [91]. Four types are recognized based on genomic sequence analysis: EMCV-1, 2, 3, and 4, each with distinct geographic distributions [92]. Rats are considered the primary wild reservoir for EMCV, and they have been implicated in outbreaks through contamination of feed and water [93,94]. Lethal EMCV outbreaks, as well as individual cases, have been reported in a wide range of mammals, including nonhuman primates [93,95–97].

Among NHPs, lethal infections have been reported in both NW and OW primates, including great apes [93,95–100]. EMCV infection frequently manifests as sudden death without prior clinical signs, although symptoms associated with cardiac insufficiency and nonspecific signs of disease may be observed shortly before death [93,98,100]. The disease is considered to be zoonotic, but clinical signs in humans are rare, and infection is more likely to result from contact with rodent excreta rather than from infected NHPs.

An early vaccination strategy used a genetically engineered attenuated Mengo virus, a closely related cardiovirus, to confer cross-protection against EMCV in olive baboons (*Papio Anubis*) and rhesus macaques. Although no virus challenge was performed in NHPs, observed antibody titers after two weeks following an IM vaccination on Days 0 and 21 containing 10^6 PFU vMC_{24} Mengo virus were expected to be protective based on the protection of pigs (*Sus domesticus*) by the same vaccine against an epizootic EMCV strain. No adverse effects were observed following immunization [101]. The EMCV-3 strain SING-M105, which was isolated from infected orangutans, has been used to develop an inactivated vaccine. This binary ethylenimine (BE)-inactivated virus vaccine induced high neutralizing antibody titers in mice when administered IM as 50 mg antigen/mouse in a 1:1 mixture with Complete Freund's adjuvant (Sigma-Aldrich, Burlington, MA, USA). This vaccine was well tolerated, but no trials have been reported yet in nonhuman primates [102]. Another inactivated vaccine has been described in Australia, which induced a consistent and high

antibody titer in all animals, including eight chimpanzees, for at least 36 months following vaccination. A 2 mL dose containing a 1:1 mixture of $10^{8.38}$ $TCID_{50}$/mL inactivated in 0.1% β-propriolactone (BPL) with the oil-based adjuvant Montanide ISA 206 (SEPPIC S.A., quai d'Orsay, Paris, France) was administered. The observed lack of correlation between body weight and degree of immune response suggests that a reduced dose may also confer adequate immunity. In the same study, but in vaccinated ungulates, it was observed that animals receiving a second dose of the vaccine after one month had higher titers throughout the study period. The chimpanzees vaccinated in this study, however, did not receive a booster vaccination. No adverse effects were observed following immunization [96]. One downside of this vaccine is the usage of BPL for inactivation, which is a suspected carcinogen [103].

Commercial porcine vaccines were available in the United States the past. One of these, EMC Vac® (Bayer Animal Health, Worthington, MN, USA), was evaluated in hamadryas baboons. In this study, two 2 mL vaccinations containing at least 5×10^6 $TCID_{50}$ inactivated EMCV-25 were administered IM 21 days apart. Five of six baboons developed antibody titers that persisted for at least six months, and no adverse effects were reported [104].

It is unclear whether vaccines based on one group confer protection against other EMCV groups. Although further research is warranted to evaluate the safety and efficacy profiles in different NHP species, current safety and efficacy data appear to be favorable for the use of EMCV vaccines in NHPs.

5.3. Hepatitis A

Hepatovirus A, or hepatitis A virus (HAV), is a virus in the genus *Hepatovirus* of the *Picornaviridae* family. NW monkeys, particularly three-striped night monkeys (*Aotus trivirgatus*) and tamarins (*Saguinus mystax*, *Saguinus labiatus*), are reported to be susceptible to experimental HAV-induced hepatitis [105,106]. OW monkeys, such as rhesus and cynomolgus macaques, exhibit greater resistance [107–109]. Subclinical HAV infection has been reported in laboratory primates, including those used for toxicology studies, and it may be more prevalent than the literature indicates and confounds their use in research studies [110]. Chimpanzees are also susceptible to experimental HAV-induced hepatitis [111]. Natural HAV infection has been reported in African green monkeys (*Chlorocebus* sp.), cynomolgus macaques, and rhesus macaques. Asymptomatic infections may occur, but reported symptoms include anorexia, lethargy, and diarrhea resulting from acute hepatitis in macaques. Although total morbidity rates are not reported, natural HAV infection has been attributed as cause of death of 13.0% (21/162) of rhesus macaques, 45.0% (9/20) of cynomolgus macaques, and 28.0% (56/200) of African green monkeys in captive colonies [112].

Isolates from night monkeys, cynomolgus macaques, and African green monkeys suggest that HAV constitutes a heterogenous group of viruses that may differ from human isolates [113–115]. A serologic survey conducted in 1980 reported high seroprevalence of hepatitis A in chimpanzees, baboons, vervet monkeys (*Chlorocebus pygerythrus*), gracile capuchins (*Cebus* sp.), and common marmosets [116]. Only few reports exist describing the transmission of HAV from NHPs to humans [117]. As a result, the zoonotic potential of simian HAV isolates and the efficacy of human HAV vaccines on simian variants remain unknown [118].

Vaccination of susceptible NHPs with a human vaccine has been proposed [119] but has not been reported. Further research is required to determine the efficacy and safety profiles of human hepatitis A vaccines in NHPs. Currently, vaccination against HAV is not recommended due to the absence of clinical symptoms associated with natural infection,

combined with a paucity of data on vaccine efficacy and safety. However, vaccination of human staff may reduce the possibility of zoonotic and reverse zoonotic infection.

5.4. Hepatitis B

Hepatitis B virus (HBV) belongs to the genus *Orthohepadnavirus* in the family *Hepadnaviridae*. HBV infection has been reported in different NHPs, including cynomolgus macaques, woolly monkeys (*Lagothrix lagotricha*), gibbons (*Hylobates* sp.) and great apes [120–128]. Hepatitis B is relatively apathogenic for NHPs, but poses a significant health risk for personnel working with NHPs. A seroprevalence of 24.4% (64/262) has been reported in apes compared to a low seroprevalence of only 0.02% (1/4543) in monkeys [122]. Natural infections among NW monkeys are not reported [129]. NHP HBV strains are reported to be nearly identical to human HBVs, although the zoonotic implications have not yet been investigated [126]. The pathology is similar to that described in humans, but progression to cirrhosis and hepatocellular carcinoma has not been reported [118].

Although immunization against hepatitis B has been proposed in chimpanzees by the EAZA BPG [19], vaccination of animals is not routinely performed. The use of a recombinant hepatitis B vaccine (Energix B®, SmithKline Beecham, Biologicals, B-1330 Rixensart, Belgium) is reported in silvery gibbons (*Hylobates moloch*). One animal received 0.5 mL of Energix B® containing 10 mg HBV surface antigen IM at 24–72 h after birth in combination with 0.1 mL HBV immunoglobulin (100 IU/mL) followed by 0.5 mL Energix B® boosters at six weeks and five months of age. The serologic response was still measurable 4.5 years after the initial vaccination. Another animal received the same immunization protocol, but without the booster at one month of age. Blood collected two years after the initial vaccination demonstrated a serologic response to the vaccine, suggesting that a single booster may also induce an adequate serological response. No adverse effects were reported in these animals [130].

Due to the limited information on vaccine safety and efficacy, no recommendations on vaccination of NHPs can be provided. The Energix B® vaccine appears to be safe in silvery gibbons, but it is unknown whether the observed response confers protection against natural HBV challenge. Instead, institutions may consider the vaccination of personnel in order to reduce the possibility of reverse zoonotic infection.

5.5. Influenza

There is a paucity of literature on natural influenza infection in NHPs. Clinical disease, as described in experimental challenges, is similar to humans, and may manifest as fever, malaise, nasal discharge, and nonproductive cough [131]. However, one must keep in mind that the high viral loads used in experimental challenge are unlikely to produce disease representative of natural infection.

Seroconversion following natural exposure to the H1, H2, H3, and H9 subtypes of influenza A virus has been reported in macaques [131]. In fact, antibodies against influenza A were demonstrated in 19.0% (128/672) of investigated macaque serum samples in Thailand [132]. Seroprevalence has been demonstrated in captive gorillas (influenza A H3N2 3.9% (3/77), influenza A H1N1 3.9% (3/77), influenza B 58.4% (45/77)), orangutans (influenza A H3N2 5.6% (10/179), influenza A H1N1 19.0% (34/179), influenza B 75.4% (135/179)), and chimpanzees (influenza A H3N2 11.2% (34/305), influenza A H1N1 71.5% (218/305), influenza B 26.2% (80/305)) [132]. Moreover, NHPs readily seroconvert after experimental inoculation with seasonal influenza virus and have been used to test candidate vaccines for strains of human and avian origin [131]. Although the efficacy of various influenza vaccines has been evaluated experimentally in NHPs, very little information exists on the efficacy of current commercial vaccines in NHPs in a natural setting.

Nevertheless, according to non-peer reviewed sources, immunization with an inactivated vaccine is generally considered to be safe in NHPs. In fact, its usage in great apes has been recommended by EAZA care manuals in early fall, prior to influenza season [18,22].

All great apes are recognized as being susceptible to influenza. However, there is a paucity of research regarding the extent of their susceptibility, the efficacy of vaccines in preventing natural infection, and the safety profiles of these vaccines across different NHP species. Vaccination of staff working with great apes constitutes an important measure and may prove more practical and impactful than vaccination of NHPs [17].

5.6. Morbilliviruses

5.6.1. Canine Distemper Virus (CDV)

Canine distemper virus (CDV) is a single-stranded RNA virus of the genus *Morbillivirus* within the family *Paramyxoviridae*. CDV infections have been reported in a wide range of carnivore species, but may also occur in NHPs. An outbreak in a large captive colony rhesus macaques resulted in the infection of approximately 10,000 animals. The reported morbidity and mortality rates in young animals were 60% and 30%, respectively, and 25% and 5% in adult animals [133]. Reported clinical signs in macaques are similar to those observed with measles infection, and include fever, exanthema, anorexia, pyrexia, swelling of the footpads, pneumonia, conjunctivitis, nasal discharge, diarrhea, and neurological symptoms [133–135].

Following a large outbreak in rhesus macaques in China, surviving animals were immunized with an inactivated suspension derived from the livers and lungs of deceased animals. This resulted in a significant decrease in CDV incidence in the colony. No information on the exact vaccine composition, dosage, or observed adverse effects is available [133].

Interestingly, it has been reported that vaccination against the measles virus may induce both cellular and humoral cross-immunity for CDV in NHPs [136]. An attenuated CDV vaccine (Vanguard® (1.0 mL, IM; Zoetis, Parsippany, NJ, USA) containing 10^3 $CCID_{50}$ attenuated CDV is reported to induce detectable antibody titers in all rhesus macaques (n = 37/37). A human measles vaccine (Attenuvax® (0.5 mL, SC; Merck & Co., Rahway, NJ, USA)) containing 10^3 $TCID_{50}$ attenuated measles virus induced antibody titers in 81% (9/11) of animals when administered once. Subsequent challenge with measles virus revealed that subclinical viremia was detectable in two of the Attenuvax®-inoculated (n = 11) and two of the single-dose Vanguard®-inoculated (n = 19) animals, but in none of the animals that received two doses of Vanguard® (n = 18) [137].

More recent research using CDV vaccines (Vanguard®) has demonstrated that half-dose vaccinations (0.5 mL) are equally effective as full doses (1.0 mL) in inducing neutralizing antibody titers when administered once. Quarter-dose vaccinations, however, were reported to be less effective than either half or full doses [138].

No adverse effects have been reported with the usage of CDV vaccines (Vanguard®) in large groups of long-tailed macaques, rhesus macaques, titi monkeys (*Callicebus moloch*), and squirrel monkeys (*Saimiri* sp.) [138].

In conclusion, commercial CDV vaccines appear to effectively and safely induce protective antibody titers in NHPs when administered twice. These vaccines may aid in reducing morbidity and mortality associated with CDV outbreaks.

5.6.2. Measles

The measles virus is closely related to the CDV virus and also belongs to the genus *Morbillivirus* within the family *Paramyxoviridae*. Humans are recognized as the only source of infection for NHPs [139]. Numerous species of OW and NW primates are susceptible to

the measles virus, with spontaneous outbreaks documented globally [140–142]. However, major measles outbreaks are increasingly rare in industrialized countries due to the reduced circulation of the virus in human populations. Additionally, quarantine and vaccination methods in NHPs, along with the vaccination of personnel, have likely contributed to this trend [139]. Despite this, sporadic cases continue to emerge each year due to factors such as immigration, travel, and an increase in vaccine refusal [143]. This underscores the need for a vaccination strategy for housed NHPs.

Various vaccine formulations are currently marketed to vaccinate against measles. Most human-attenuated live vaccines are combined preparations for measles, mumps, and rubella (MMR) (see Section 5.6.3.), but monovalent vaccines are marketed in some countries [144]. Vaccination of rhesus (n = 222) and pigtailed macaques (*Macaca nemestrina*) (n = 36) with a single dose of human monovalent measles vaccine (MVac® (Serum Institute of India, Pune, India)), containing 10^3 $CCID_{50}$-attenuated measles virus, resulted in seroconversion of all rhesus macaques and 85.7% (30/35) of pigtailed macaques. Moreover, antibody titers were observed to wane more quickly in pigtailed macaques. No conclusions on vaccine effectiveness can be drawn, as no disease challenge was conducted in these animals. No adverse effects were reported following immunization [144].

Following IM vaccination (0.5 mL, Attenuvax®), immunity has been reported to exceed 11 years in Western lowland gorillas, but only 75% (21/28) of animals are reported to seroconvert following vaccination. No adverse vaccination reactions have been observed [145]. In vaccinated wild mountain gorillas (*Gorilla beringei beringei*), a positive titer has been demonstrated in only one of five animals after 14 years [146].

Vaccination against the measles virus has been demonstrated to confer protection against other morbilliviruses, such as canine distemper virus (CDV). Notably, the more affordable CDV vaccine has also been demonstrated to confer protection against the measles virus (see Section 5.6.1.).

Other methods of vaccine administration have been explored. For example, a single-dose, attenuated, dry powder vaccine has been developed for respiratory administration. These vaccines confer protective antibodies that were reported to still be effective one year following vaccination in cynomolgus macaques when at least 10^3 PFU-attenuated measles virus are administered intratracheally. No adverse effects were reported [147,148]. Recently, microneedle patches that contain micron-sized polymer needles have been developed. In rhesus macaques, application of these patches resulted in protective antibody titers. These patches contained 4.3×10^3 $TCID_{50}$ of attenuated measles virus and 3.6×10^3 $TCID_{50}$ of attenuated rubella virus. The patches were applied on the inner thigh for 15 min. Following application, faint puncture marks and transient erythema were noted [149,150]. Both microneedle patches and dry powder vaccines offer a single-dose vaccination without the use of syringes. Moreover, both vaccines are thermostable, facilitating their use in developing countries [147,150].

It is recommended not to use live attenuated measles vaccines in callitrichids, as it has been suggested that this may lead to disease and even death [9]. Inactivated vaccines may be available in some countries but have been discontinued in others due to associated health risks and poor protection compared to the live vaccine in humans [9]. Another consideration is the observation that measles vaccination may interfere with tuberculin skin testing [151]. Moreover, in line with other live vaccines, vaccination with a live measles vaccine should not be administered concurrently with other vaccines or to animals with active infections, immunosuppressed individuals, or pregnant animals [17].

Maternal antibodies should be considered in young animals. For example, it has been proposed that rhesus macaques under six months of age do not respond to vaccination, likely due to interference of maternal antibodies [139]. In great apes, maternal antibodies

may persist until 15 months of age [145]. Vaccination before this period may be considered, but an extra booster after waning of maternal antibodies is advisable [152].

In conclusion, veterinary CDV vaccines are considered to be at least equally, if not more, efficacious than human vaccines, and generally cost less. In fact, CDV vaccines are likely more effective than monovalent human measles vaccines in OW monkeys [137,145,146]. A two-dose vaccination schedule, administered three months apart, was demonstrated to be most effective in rhesus macaques [137]. Moreover, the use of half-dose vaccinations at a three-month interval further reduces costs by 50% and is considered to be equally effective [138]. Unfortunately, a paucity of literature exists on the immunization of most NW primate species against measles. Due to the high susceptibility of callitrichids to clinical disease, however, it is advisable to vaccinate with a killed vaccine, as well as to vaccinate personnel working with NHPs against the disease [153].

5.6.3. Measles, Mumps, and Rubella (MMR)

No reports exist on natural mumps infection in NHPs, although experimental infection has been achieved in common marmosets and in cynomolgus and rhesus macaques [154,155]. Similarly, natural rubella infection has not been described, but experimental infection has been reported in a range of OW primates [156–158]. The great ape TAG, however, notes that both diseases may cause serious symptoms in apes [17].

There is no literature describing the use of human multivalent MMR vaccines in NHPs, and therefore no information on their efficacy or safety profiles is available. Nevertheless, their usage is advised by the great ape TAG, as they are widely accepted to be safe in great apes [19]. However, MMR vaccination is contraindicated in pregnant animals due to risk of fetal infection. The recommended vaccination protocol consists of a vaccination at 15 months of age, followed by a booster immunization 6–7 years later [16].

An MMR vaccine may be considered for great apes, but little is known about its efficacy, duration of protection, and safety profile. Overall, due to the decline in the incidence of human disease achieved through vaccinations, effective preventive health protocols for NHPs, and adherence to personal protective procedures by staff, NHPs are often not routinely vaccinated for measles, mumps, or rubella [63].

5.7. Poliomyelitis

The poliovirus belongs to the genus *Enterovirus* within the family *Picornaviridae*. Like other *Enteroviruses*, poliovirus is mainly transmitted by the fecal–oral and respiratory routes [159]. Following infection, the virus replicates in the gastrointestinal or respiratory epithelium, and then spreads to other organs, including the central nervous system. Here, motor neurons are destroyed, causing acute paralytic disease [160]. Reports on clinical disease resulting from natural poliovirus infection are lacking. Experimental infection of macaques (*Macaca* sp.) demonstrates similar disease progression to humans, which is characterized by acute flaccid paralysis [161]. NW primates appear to be unsusceptible to the disease, even when challenged experimentally [162,163]. Clinical poliomyelitis has been reported in non-peer reviewed literature in chimpanzees, gorillas, and orangutans [17,19,21].

The Global Polio Eradication Initiative (GPEI), launched in 1988, successfully eradicated serotypes WPV2 and WPV3 in 2015 and 2019, respectively [159]. Nevertheless, WPV1 is still sporadically reported in the Middle East and Africa [164,165].

There are attenuated, oral, trivalent polio vaccines and enhanced potency inactivated polio vaccines (eIPV) available. In humans, both vaccine types are administered at 3, 6, and 9 months of age, followed by a booster immunization at 2 years of age [16]. The chimpanzee BPG recommends three doses of live trivalent polio vaccine at 2–3-month intervals, with the first vaccine administered at 3 months of age. Oral boosters are administered after

4–6 years. When using the oral vaccine, it must be administered to all animals in the group at the same time [19].

Although polio vaccination has been historically recommended for great apes, the cost of vaccination and the decreasing risk of infection likely outweigh the risk of exposure and infection in most countries.

5.8. Poxviruses

5.8.1. Cowpox

Cowpox infection is caused by the cowpox virus, which belongs to the genus *Orthopoxvirus* in the family *Poxviridae*. The disease is primarily transmitted by rodent vectors and has been reported in both OW and NW primates [166–168]. NW primates may develop pox-like lesions on the face, scrotum, soles, and palms [169,170]. High mortality rates have been reported in NW primates due to the infection [171,172]. Cowpox has also been reported in different macaque species [167,173]. An outbreak in Tonkean macaques (*Macaca tonkeana*) in a zoo in Italy resulted in the death of 12 animals. Reported symptoms include depression, nausea, respiratory distress, neurologic disease, and skin and mucosal lesions [173]. Moreover, the disease is considered to be zoonotic. Not only through transmission by rodent vectors, but asymptomatic zoonotic infection from a NHP to a human caretaker has also been reported during the outbreak in Tonkean macaques [174].

Vaccination against cowpox has been reported in capuchins in at least one EAZA zoo [10]. Moreover, a modified vaccinia virus Ankara (MVA) vaccine (0.5 mL, SC; Bavarian Nordic, Kvistgaard, Denmark) containing 0.5×10^8 infectious units of MVA-BN has been used to protect remaining Tonkean macaques during the aforementioned outbreak [173]. Here, the vaccine was administered twice, one month apart, according to the manufacturer's immunization protocol. All vaccinated animals (*M. tonkeana* (n = 4), *M. fascicularis* (n = 5), *M. sylvanus* (n = 1) demonstrated a 2–5-fold increase in IgG titer, and no adverse effects were reported [173].

Although no information is available about safety profiles in other NHP species, initial reports are promising. Because the vaccination was administered relatively late during the Tonkean macaque outbreak, it is difficult to assess the vaccine's efficacy. Nevertheless, an MVA vaccine may be considered for use in NHPs at risk of cowpox infection.

5.8.2. Mpox

Monkeypox virus (MPXV), also known as mpox, is an increasingly relevant zoonotic virus belonging to the genus *Orthopoxvirus* in the family *Poxviridae*. Two geographically distinct clades are recognized. Clade I (CI) is endemic to the tropical forests of Central Africa, and it is considered to be more virulent [175]. Clade II (CII), endemic from Sierra Leone to Cameroon (CIIa), is considered to be less virulent, but is implicated in a recent multinational outbreak involving extensive person-to-person transmission (CIIb) [176,177]. The exact reservoir of this disease has not been determined, but different rodent species have been proposed [178,179]. The disease was first described in captive cynomolgus macaques [180], and has since been described in rhesus macaques, common squirrel monkeys (*Saimiri sciureus*), Hamlyn's monkeys (*Cercopithecus hamlyni*), common marmosets, gorillas, chimpanzees, orangutans, and a lar gibbon (*Hylobates lar*) [181–183]. In macaques, reported symptoms include vesiculopustular and papular skin lesions, facial and cervical edema, dyspnea, bloody diarrhea [180,181]. In orangutans, erythema and purulent nasal discharge have been reported [182]. An outbreak of CI MPXV in a group of 23 captive chimpanzees resulted in an 87% (20/23) morbidity rate and a 10% (2/20) mortality rate [184]. Reported clinical symptoms in chimpanzees include exanthema, cutaneous abscessation or

eschar formation, lethargy, facial and perilaryngeal edema, rhinitis, diarrhea, dysphagia, and dyspnea [183,184].

ACAM2000® (Emergent BioSolutions, Gathersburg, MD, USA) is a replication-competent vaccinia virus that has been investigated as a vaccine for monkeypox. It has been demonstrated that the administration of 2.5–12.5 $\times$ 10^5 PFU ACAM2000® by means of scarification significantly reduces clinical disease and viremia in cynomolgus macaques following MPXV challenge. Following scarification, red patches were observed on all animals at the vaccination site four days after vaccination. Dry scabs persisted for approximately three weeks. No other adverse effects were observed [185,186].

The LC16m8 vaccine contains a minimally replication-competent vaccinia virus derived from the Lister strain, which has been used in first-generation vaccines. A single vaccination in cynomolgus macaques with >1 $\times$ 10^8 PFU/mL LC16m8 by means of scarification was demonstrated to confer protection against MPXV challenge for at least one year following vaccination. Although no adverse effects are mentioned, it can be assumed that similar red patches and scab formation occurred at the site of scarification [187]. LC16m8 is considered to be safer than ACAM2000® due to the risk of progressive vaccinia [188].

A commercial replication-deficient MVA-based vaccine (JYNNEOS® (Bavarian Nordic, Martinsried, Germany)) was effectively used in humans during the 2022 CIIb monkeypox outbreak in the United States [189]. In cynomolgus macaques, a prime-boost vaccination regime using 0.5 mL (>0.5 $\times$ 10^8 infectious units of MVA-BN) SC Imvamune® (Bavarian Nordic, Martinsried, Germany), which is based on an MVA strain, was demonstrated to confer significant protection against MPXV challenge. Protection following single vaccination was reported to be inferior, and no adverse effects were reported [185]. Administration of MVA (0.5 mL, SC, 0.7 $\times$ 10^8 PFU/dose, 26 days apart) was demonstrated to confer complete protection to lethal MPXV challenge in cynomolgus macaques, although clinical signs were reported to be severe [190]. The same study, however, also demonstrated that the administration of an mRNA-1769 vaccine (0.5 mL, IM, 150 mg/dose, 26 days apart) confers superior protection to MVA. In fact, a 10-fold decrease in lesions was observed mRNA-immunized animals, along with a shortened duration of disease, and reduced circulating and mucosal viremia. Moreover, the mRNA vaccine induced a greater humoral response, and neutralizing antibodies were broadly reactive against other *Orthopoxvirus* species. No adverse effects were reported for either vaccine in this study [190].

Ad35 vector-based subunit vaccines expressing two (5 $\times$ 10^{10} viral particles (vp)/dose) or four (5 $\times$ 10^8 vp/dose) vaccinia antigens have been used in experimental settings. These vaccines are reported to confer better protection than MVA vaccines but inferior protection to ACAM2000® when administered twice IM four weeks apart. No adverse effects were reported in this study [191].

It has been proposed that second- and third-generation vaccines may not only be used for pre-exposure immunization, but could also confer protection against disease or death when administered within 4–14 days after MPXV exposure [192].

In conclusion, ACAM2000® is considered to confer near-complete protection against MPXV infection, whereas MVA and LC16m8 provide significant but incomplete protection [191]. Moreover, both mRNA vaccines and Ad35 vector-based subunit vaccines constitute promising vaccine candidates, and further research should be conducted.

5.9. Rabies

The rabies virus, officially classified as *Lyssavirus rabies*, is the most notable species of the genus *Lyssavirus* in the family *Rhabdoviridae*. Infection with rabies most commonly occurs due to penetration of infected saliva into wounds after bites of infected animals [193]. The disease is characterized by the development of severe nervous symptoms that lead to

paralysis and death [194]. Rabies has been reported in a wide range of OW and NW NHP species [151,195–198]. In fact, common marmosets are reported to be a potential source of exposure for humans [199,200].

Currently, rabies virus is regarded as a pathogen of diminishing importance in Europe; however, it remains endemic in most countries worldwide. Even nations deemed free of rabies may still host endemic bat lyssaviruses, and the possibility of reintroduction through the pet trade or wildlife persists. In rabies-endemic countries, outdoor enclosures constitute an important risk factor for rabies in captive NHPs, as exposure to rabid wildlife may occur [194,197,199].

Attenuated live vaccines are commercially available but must never be used in NHPs as their efficacy and risk of return to virulence has not been evaluated [59]. Killed virus preparations for vaccination against rabies are widely available and are considered to be safe in NHPs [16,59,201].

Little literature evaluating vaccine efficacy exists, but subcutaneous (SC) vaccination with a two-dose regimen of 1 mL Defensor® (SmithKline Beecham, West Chester, PA, USA) containing $>10^{7.35}$ $TCID_{50}$ per vaccination with a 30-day interval has been demonstrated to induce significant neutralizing antibody titers in pigtailed and rhesus macaques, without observed adverse effects [201]. Another study conducted in rhesus-cynomolgus macaque hybrids evaluated a single 1.0 mL SC injection of Rabisin® (Boehringer Ingelheim, Wanchai, Hong Kong), containing >1 I.E. rabies GS-57/Wistar strain glycoprotein. A seroconversion rate of 72% (26/36) 2.5–6 years following a single immunization was demonstrated, and no adverse effects were observed [202]. However, it is uncertain whether these titers confer protection against natural rabies virus challenge.

A variety of other vaccine protocols are reported in different species, but these are not supported by evaluation of plasma titers or challenge studies. The current recommended protocol according to the AZA care manuals for colobus monkeys and hamadryas baboons consists of 1 mL IM at 6–12 months of age, followed by a booster vaccination every 1–3 years [12,15]. Similarly, the capuchin BPG recommends vaccination with a killed vaccine every three years [10]. In great apes, it is recommended to follow the human vaccination regime. The first dose may be given from four months of age, consisting of vaccines at Days 0, 7, and 21–28, followed by a booster after one year, and subsequent boosters every three years [16–18]. It has been proposed that the vaccine dosages be adjusted to account for the smaller size of NW and OW monkeys, with recommended doses of 0.05–0.1 mL for callitrichids, 0.25 mL for medium-sized primates, and 0.5 mL for larger primates [63]. As with the similar proposal for tetanus vaccinations, efficacy studies have not been conducted for most species, nor have studies been performed with these reduced dosages. Consequently, these recommendations should be interpreted with caution until efficacy studies become available.

In conclusion, preventative measures are essential to prevent rabies in endemic areas, particularly when NHPs are housed with outdoor access. Vaccination may also be considered in areas deemed free of rabies when exposure to other sources, such as bats or inadequately screened imported animals, is likely. When vaccinating, it is imperative to use killed vaccines, as they are considered to be safe and effective in NHPs. Given the limited literature on vaccine efficacy in most species, it is prudent to adopt a cautious approach. A recommended protocol includes three initial vaccinations: the first dose, followed by subsequent doses one week and three to four weeks later, and a final dose one year after the initial vaccination. Booster immunizations are recommended to be administered every three years, although this is only based on expert opinion [10,12,15–18]. More frequent vaccinations may be warranted based on clinical experience and specific risk factors.

5.10. Saimiriine gammaherpesvirus 2 (SaHV2; HVS)

Saimiriine gammaherpesvirus 2, commonly known as herpesvirus saimiri (HVS), belongs to the genus *Rhadinovirus* within the subfamily *Gammaherpesvirinae* of the family *Orthoherpesviridae*. It is reported that squirrel monkeys are naturally infected through saliva within the first two years of life [203]. Following infection, the virus persists in the host for life, primarily within T-lymphocytes [204]. While the virus is not associated with clinical disease in squirrel monkeys, it can induce T-cell leukemia and lymphoma in other neotropical primates [204–207]. Three HVS subtypes are recognized, all of which have been reported to be able to cause T-cell lymphoma in cotton-top tamarins. Subtypes A and C may also induce T-cell lymphoma in marmosets, and subtype C can do so in macaques [208]. Additionally, malignant lymphoma has been reported following incidental infection of night monkeys, and following inoculation of marmosets, howler, and spider monkeys [208].

Passive immunization has been achieved using heat-killed, formaldehyde-treated HVS, which protected cotton-top tamarins against tumor formation [207]. No other vaccine trials have been reported, and consequently, no commercial vaccines are available. To prevent lethal infection, it is advisable to avoid cohabitation of squirrel monkeys with susceptible neotroptical primate species.

5.11. SARS-CoV-2

Severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) is an enveloped, single-strained RNA virus belonging to the genus *Betacoronavirus* in the family *Coronaviridae*. SARS-CoV-2 infections have been documented in both captive and wild NW and OW primates, including great apes. Reported clinical signs in Western lowland Gorillas include coughing, nasal discharge, lethargy, and hyporexia [209]. In macaques, SARS-CoV-2 infection remains limited and mild despite the administration of a high viral dose via bronchoscopy. This is thought to be due to structural differences in the upper respiratory tract. The virus is quickly cleared within a short period. Long COVID cases are currently only described in experimental settings in NHPs [210].

In 2021, a SARS-CoV-2 vaccine was developed for use in carnivores (Carnivac-Cov®) [211]. No reports on its use in NHPs are available; instead, human vaccines are recommended, as these have been reportedly used in NHPs without adverse effects (1.0 mL, Sc or IM, Zoetis International) [212]. Nevertheless, the efficacy of human vaccines in NHPs remains poorly understood.

There are vaccines available against coronaviruses other than SARS-CoV-2, e.g., feline, canine, bovine, porcine, and avian coronaviruses. There is no evidence to suggest cross-protection provided by these vaccines against SARS-CoV-2. In fact, cross-protection may be low even among various variants of concern within the SARS-CoV-2 virus. Moreover, some of these vaccines against other coronaviruses are live-attenuated vaccines and may present a disease risk with off-label use in NHPs [209,213].

SARS-CoV-2 generally causes mild disease in NHPs, and the decision to vaccinate may largely depend on individual factors contributing to susceptibility, ease of administration, incidence of disease in the geographic area, and vaccination status of staff. Moreover, the vaccination of staff working with great apes should be considered and constitutes an important preventative measure [209].

5.12. Simian retrovirus (SRV)

Simian retroviruses (SRVs), historically known as simian type-D retroviruses, belong to the genus *Betaretrovirus* within the subfamily *Orthoretrovirinae* of the family *Retroviridae*. Asian macaque species are identified as the natural hosts for SRV [214]. SRV infections have been reported in primate research centers around the world [215–217]. Infected animals

may develop an AIDS-like syndrome as a result of lymphocyte suppression [218–221]. To date, eight serotypes have been described, each associated with their own clinical symptoms. SRV-1 may cause anemia and granulocytopenia [219]; SRV-2 has been related with retroperitoneal fibromatosis and may lead to tumor formation [222]; SRV-3 is highly similar to SRV-1 and suppresses T-lymphocytes [223]; SRV-4 has been associated with multifocal lymphoplasmacytic and histiocytic inflammation [217]; SRV-5 may cause B-lymphocyte suppression in various tissues [224]; SRV-6 and SRV-7 are only mentioned sporadically; and SRV-8 has been associated with anemia, weight loss, and persistent unresponsive diarrhea [217]. SRV is considered to be zoonotic, but no clinical disease has been reported in humans [225].

To date, two vaccination strategies have been explored for SRV. The first involves a formalin-inactivated whole SRV-1 vaccine. In this study, each rhesus macaque received three IM immunizations 18, 15, and 9 weeks prior to SRV-1 challenge. These immunizations contained 1 mg of sucrose gradient-purified SRV-1 with threonyl muramyl–dipeptide adjuvant. Transient lymphadenopathy was observed following immunization, likely attributable to the used adjuvant. This regimen resulted in the protection of 80% (5/6) of macaques against viremia and disease upon challenge with 2×10^5 syncytia-inducing units of SRV-1 [226]. The second strategy utilizes a vaccinia virus recombinant vaccine expressing SRV envelope glycoproteins gp70 and gp22. In contrast to the formalin-inactivated vaccine, cell-mediated cytotoxicity was elicited by the recombinant vaccine [227,228]. A vaccinia virus recombinant vaccine expressing SRV glycoproteins from serotype 1 or 3 was demonstrated to induce protection against SRV-1. To this end, rhesus macaques were immunized with 10^8 PFU of SRV-1 (n = 3) or SRV-3 (n = 1) recombinant virus by means of skin scarification at 14, 8, and 2 weeks prior to IV challenge with 2×10^5 syncytium inducing units of SRV-1. Although this method effectively protected animals against SRV-1 and SRV-3, serum from these animals failed to neutralize the more genetically distant SRV-2 in vitro [227].

Future research may focus on the development of a recombinant vaccine that provides cross-protection between all eight serotypes. The vaccines have not been widely applied, likely due to the absence of a commercial vaccine, costs, and limited availability of data on safety profiles and in vivo efficacy [214].

5.13. Yellow Fever

The yellow fever virus (YFV), classified under the genus *Orthoflavivirus* within the family *Flaviviridae*, causes zoonotic disease and is transmitted through mosquito vectors. YFV is reported to cause severe epizootic hemorrhagic fever syndromes in both NW and OW primates. Documented mass mortality events have occurred among wild NW primates, such as howler, spider, and squirrel monkeys [229–232]. Due to their high susceptibility, epizootic events in NHPs are used as epidemiological indicators for human yellow fever outbreaks [233]. However, susceptibility varies among NW primates, with some species exhibiting minimal or no symptoms, and even acting as reservoirs [233,234]. Howler monkeys are considered to be the most susceptible of all NW primates [234]. OW primates typically remain asymptomatic whilst experiencing viremia [235].

The human yellow fever vaccine is an attenuated vaccine that has been successfully used for over 80 years. The attenuated strain, designated 17D, has lost its viscerotopism and the ability to be transmitted by the domestic mosquito vector *Aedes aegypti* [236]. A substrain, 17DD, derived from the 17D strain, is employed in some vaccines [237]. Immunity in humans following a single vaccination is reported to persist for at least 35 years, and it is likely to be lifelong [238].

Rhesus and cynomolgus macaques are the only WHO-approved animal models for YFV vaccine safety testing, and as a result, commercial vaccines are considered to be safe in these species [239]. The vaccination of golden (*Leontopithecus rosalia* (n = 3)), golden-headed (*Leontopithecus chrysomelas* (n = 6)), and black lion tamarins (*Leontopithecus chrysopygus* (n = 2)) with the 17DD substrain has been investigated to reduce the sylvatic transmission cycle in the Americas. Animals were vaccinated with a single IM dose of 1×10^3 or 5×10^3 PFU live-attenuated 17DD YFV. No vaccine-associated adverse effects were observed, and the transmission cycle was effectively interrupted [236]. Moreover, the 17DD vaccine has been evaluated for safety in howler monkeys, with no adverse effects reported at the studied dosages (up to $10^{3.7}$ PFU) [240]. No virus challenge was conducted, but the vaccination elicited the production of neutralizing antibodies, similar to what was observed in rhesus macaques vaccinated with the 17D vaccine [240,241].

Although the literature is limited for most NHP species, current research suggests that human YFV vaccines, or at least the 17DD substrain vaccines, are both safe and efficacious in OW and NW primates. Therefore, their use should be considered in endemic areas. Vaccines may be used to prevent epizootic outbreaks among NHPs and may also serve to limit the YFV reservoir, thereby contributing to public health.

6. Future Research

Although NHPs have been used frequently in vaccine studies, data on vaccine efficacy in a field setting, adverse effects, and the influence of different vaccination regimens on the induction of protective immunity are lacking for most NHP species. Novel vaccine trials can shed light on some of these factors but are often conducted in small animal groups of a limited number of species under highly controlled circumstances. As a result, the results may not always accurately reflect vaccine effectiveness under field conditions in a range of NHP species. Moreover, the number of NHP species, types of vaccines and their respective administration routes, booster protocols, etc., are not all feasibly assessable under experimental conditions. To bridge this gap more effectively, a collaborative effort should be made by clinicians to generate such data. Detailed record keeping is essential to this research, as conclusions will likely need to be drawn based on multiple years of retrospective data. For example, the veterinary clinician should make note of the type, batch number, and the manufacturer of the vaccine, as well as the way of administration in case of injectable products. Adverse effects following vaccine administration should be noted. Serological surveys during routine health checks may aid in subsequently evaluating vaccine efficacy, although one must keep in mind that neutralizing antibody titers and protective immunity do not always directly correlate. Preferably, all data should be uploaded to a worldwide accessible information system, e.g., zoological information management system (ZIMS). This facilitates sharing of information between zoological institutions, allowing clinicians to more easily identify species- or context-specific differences in vaccine efficacy and safety profiles.

7. Conclusions

This review synthesizes the current literature on non-experimental vaccination options for captive NHPs. Literature search reveals large gaps in information on vaccine efficacy and safety in many NHP species, as well as gaps in information about the occurrence of zoonotic disease in NHPs. For many diseases in NHPs (e.g., herpes B, Zika virus, simian immunodeficiency virus, etc.) no effective vaccines have been developed. In instances where vaccines are available, however, little information is often available regarding safety and efficacy profiles in different NHP species. Nevertheless, the off-label use of vaccines should be considered in all captive NHP colonies. There is no universal vaccination

regimen, and protocols should be based on a thorough risk assessment and comply with local regulations. Additionally, institutions are encouraged to adopt training programs and facility modifications that allow safe access to animals, facilitating necessary medical procedures, including vaccination. Furthermore, institutions should establish biosecurity protocols to safeguard the health of both animals and staff. The immunization of personnel may constitute a critical component of an institution's biosecurity plan, as it may reduce the risk of zoonotic and reverse zoonotic infection. In order to address the paucity of literature on vaccine efficacy and safety in a wide range of NHP species, veterinary clinicians may contribute by accurate record keeping in a shared database. By accumulating large amounts of data under field conditions, trends in vaccine efficacy and adverse effect profiles may be identified.

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