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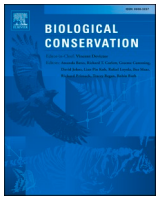

Perspective

Vaccination of endangered wildlife as a conservation tool: Hindsights and new horizons in the pandemic era

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ABSTRACT

Vaccines are an established conservation tool that can reduce the threat of infectious disease in endangered wildlife populations. Vaccines exist for many infectious pathogens, and at a time of rapid technological advances in vaccinology, developing vaccines and vaccination programs for free-living endangered wildlife could help efforts to prevent extinctions from disease threats. Vaccination efforts could focus on protecting members of the target species or could be directed at reservoir populations to prevent pathogen spillover. Vaccination strategies need to be substantiated by research on safety and effectiveness, include risk and feasibility assessments, account for differences in host biology and disease epidemiology, and align with relevant regulatory frameworks. Engagement with stakeholders and the public is important to ensure the success of endangered species vaccination programs. Challenges such as funding, regulation, and societal acceptance are barriers to progress in vaccination programs for some species and geographic regions. We recommend the development of scientifically based international guidelines and a transdisciplinary forum with a specific emphasis on endangered wildlife vaccination. New technologies could be used collaboratively to prevent transmission of diseases for which vaccines are not currently available. Careful approaches and enhanced collaborations could help ensure the successful development of wildlife vaccination programs and promote resilience of endangered wildlife populations to increasing anthropogenic and environmental stressors on biodiversity.

1. Introduction

Effective use of tools designed to address continued global threats to biodiversity could help reduce rates of global species extinctions. Infectious diseases are increasingly recognized as a threat to many endangered taxa, with a wide range of viral, bacterial, protozoal and fungal pathogens causing population declines and posing extinction threats (Heard et al., 2013; Gupta et al., 2020). Non-infectious diseases, such as toxicoses following exposure to natural and synthesized toxins, have also caused population declines, such as diclofenac killing vultures and marine toxins increasing mortality and decreasing reproduction in manatees and cetaceans (Scott et al., 2021; Oaks et al., 2004). Many infectious diseases can be prevented using vaccines, and the current emergency vaccination of California condors (*Gymnogyps californianus*) against highly pathogenic avian influenza (HPAI) highlights the use of vaccines as a tool to protect endangered wildlife from infectious disease threats (Kozlov, 2023; World Organization for Animal Health, 2024).

Concerns about disease remain high for many species because changes in anthropogenic and environmental stressors are likely to increase disease susceptibility and exacerbate the negative effects of disease outbreaks on population viability. In several endangered populations, disease outbreaks pose an imminent extinction risk. In addition to the HPAI threat to California condors, outbreaks of rabies and canine distemper virus (CDV) pose immediate threats to Ethiopian wolves (*Canis simensis*) (Sillero-Zubiri et al., 2016) and, in the Russian Far-East, small populations of Amur tigers (*Panthera tigris tigris*) are

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unlikely to survive without protection against CDV (Gilbert et al., 2015, 2020). For other endangered species, diseases may contribute to extinction risk by triggering declines that increase vulnerability of the population to other stochastic factors (Clifford et al., 2006; Cleaveland et al., 2007; Dietz et al., 2019).

Although vaccines have been demonstrably successful in reducing levels of infection in wildlife reservoirs (e.g. vaccination of wild canids against rabies, as in Maki et al., 2017, and several wildlife species against bovine tuberculosis, as in Buddle et al., 2018), vaccination of endangered species is rarely undertaken (Cleaveland, 2009). The paucity of vaccination programs for wild endangered species arises largely from concerns and challenges around vaccination of rare animals (Walsh et al., 2017). Many of these concerns, however, could be mitigated by recent advances in vaccinology, vaccine delivery, wildlife handling, and in the design and evaluation of interventions that make vaccination a feasible contemporary option for protecting endangered populations against disease (Walsh et al., 2017). Vaccination against disease may offer a direct and immediate conservation strategy for maintaining viable populations and buy time to address more complex anthropogenic or cumulative stressors such as habitat loss, trade, human-wildlife conflict and climate change.

Many diseases threatening endangered species can be prevented using vaccines or have potential to be prevented using vaccines (Tables 1, 2). Some vaccines already exist to protect domestic animals or humans and have been deployed in taxonomically related endangered wildlife species, including vaccination of great apes (Hominidae) to protect against polio and measles (Hastings et al., 1991; Goodall, 1983), vaccination of endangered carnivores to protect against rabies and CDV (Haydon et al., 2006; Knobel et al., 2008; Marino et al., 2017), vaccination of Hawaiian monk seals (*Neomonachus schauinslandi*) against CDV (Robinson et al., 2018), and vaccination of endangered felids (Felidae) to protect against feline leukemia virus (FeLV) (Cunningham et al., 2008; Nájera et al., 2021). Novel vaccines are also being developed for endangered species to counter a specific disease threat. These include vaccines to protect Tasmanian devils (*Sarcophilus harrisii*) against a transmissible facial tumor (Pye et al., 2021), bats against the fungal disease, white-nose syndrome (Rocke et al., 2019), great apes against Ebola virus (Walsh et al., 2017) and Indian yellow-nosed albatross (*Thalassarche carteri*) chicks against avian cholera (Bourret et al., 2018). Wildlife vaccination strategies have also been implemented indirectly as part of novel approaches to the conservation of endangered species. For example, prairie dogs (*Cynomys* spp.) have been vaccinated against plague (*Yersinia pestis*) to reduce the risk of pathogen transmission to the endangered black-footed ferret (*Mustela nigripes*) and sustain prairie dog populations which ferrets depend on for both prey and habitat (Rocke et al., 2017; Rocke, 2023).

The use of vaccines for endangered species conservation has been well established in mammal and bird populations in zoological collections (e.g. Georoff et al., 2020). However, conservationists need to consider many factors and face further challenges in making decisions regarding vaccination and implementing vaccination programs for free-ranging endangered wildlife (refer to Box 1 and 2 for in depth examples). Here we discuss these factors and challenges to highlight new opportunities for conservation of wild animals in the future. We do not provide an exhaustive review of wildlife vaccination, nor do we specifically address vaccination of endangered species in captivity. Rather, we aim to provide a contemporary perspective on wildlife vaccination to support its consideration as an accessible and feasible tool for addressing a wide range of disease problems that threaten endangered species and to identify future directions and priorities for its application.

2. Challenges and considerations for vaccination of endangered wildlife

Before a decision is made to vaccinate an endangered species, the aims and outcomes of vaccination, as well as the challenges, need to be

Table 1
Examples of some recent vaccinations of free-living endangered wildlife illustrating the range of diseases of conservation concern that are preventable by vaccination.

Disease/agent	Endangered species	Vaccine types available	References
Avian influenza virus	California condors, USA	Protein; commercially available	US Fish and Wildlife Service, 2024a
	Threatened seabirds, New Zealand	Inactivated; recombinant	New Zealand Department of Conservation, 2024
Canine distemper virus	African wild dog, Tanzania	Modified live; sub-unit CDV-ISCOM; multivalent; commercially available	Philippa, 2007; van de Bildt et al., 2002; Connolly et al., 2013
	Black-footed ferret, USA	Canarypox-vectored recombinant; monovalent; commercially available	Rocke, 2023
	Hawaiian monk seal, USA	Canarypox-vectored recombinant; monovalent; commercially available	Baker et al., 2017; Robinson et al., 2018
	Catalina Island fox (*Urocyon littoralis catalinae*), USA	Canarypox-vectored recombinant; monovalent; commercially available	Clifford et al., 2006; Kapil and Yeary, 2011
Feline viruses (i.e., Feline Leukemia Virus, Feline Calicivirus)	Florida panther (*Puma concolor couguar*), USA	Inactivated; monovalent; commercially available	Cunningham et al., 2008
	Iberian lynx (*Lynx pardinus*), Spain	Canarypox-vectored recombinant; monovalent; commercially available	Nájera et al., 2021
Lumpy skin disease virus	Livestock (to protect banteng, gaur), Cambodia	Attenuated live; commercially available	Porco et al., 2023
Measles virus	Mountain gorillas (*Gorilla beringei beringei*), Rwanda	Attenuated live; monovalent	Hastings et al., 1991
Peste des petits ruminants virus	Livestock (to protect saiga antelope), Mongolia	Not specified	Pruvot et al., 2020
Polio virus	Chimpanzees (*Pan troglodytes*), Uganda	Not specified	Goodall, 1983; Woodford et al., 2002
Rabbit hemorrhagic disease virus 2	Riparian brush rabbits (*Sylvilagus bachmani*), USA	Inactivated bivalent;, commercially available	Russell et al., 2024
Rabies virus	African wild dog, Tanzania/Kenya	Inactivated; monovalent; commercially available	Vial et al., 2006; Knobel et al., 2002; Connolly et al., 2015
	Ethiopian wolf, Ethiopia	Inactivated; monovalent; commercially available	Knobel et al., 2008
Yellow fever virus	Golden lion tamarins (*Leontopithecus rosalia*), Brazil	Attenuated live; commercially available	Dietz et al., 2019; Tavares da Silva

(*continued on next page*)

Table 1 (*continued*)

Disease/agent	Endangered species	Vaccine types available	References
			Fernandes et al., 2021
Anthrax (*Bacillus anthracis*)	Black rhinoceros, cheetah, South Africa	Attenuated live spore; monovalent; commercially available	Turnbull et al., 2004
Plague (*Yersinia pestis*)	Black-footed ferrets, USA	Recombinant protein	Rocke et al., 2008; Rocke, 2023
	Utah prairie dog (*C. parvidens*), USA	Poxvirus-vectored recombinant	Rocke et al., 2017
Erysipelothrix rhusiopatheae	Kakapo (*Strigops habroptila*), New Zealand	Bacterin	Gartrell et al., 2005
Chlamydia pecorum	Koala (*Phascolarctos cinereus*), Australia	Recombinant; ISCOM adjuvant; experimental	Carey et al., 2010; Waugh et al., 2016
White-nose syndrome (*Pseudogymnoascus destructans*)	Bats, USA	Poxvirus-vectored recombinant; experimental	Rocke et al., 2019
Devil Tumor Disease	Tasmanian devils, Australia	Adenoviral-vectored recombinant; experimental	Conroy, 2023

Table 2
Examples of diseases in endangered wildlife that vaccinations may help control.

Disease agent	Endangered species	Development status	References
Avian influenza virus	Rare pinnipeds	Commercially available licensed for birds.	Gadzhiev et al., 2024a, 2024b
Botulism (*Clostridium botulinum*)	Laysan duck (*Anas laysanensis*), USA	inactivated toxin	Work et al., 2010
Chytrid fungus Batrachochytrium dendrobatidis	Amphibians	Experimental killed vaccine	McMahon et al., 2014
Canine distemper virus (oral delivery)	Threatened carnivores	No current program	
Canine distemper virus	Amur tiger, Russia	Modified live, multivalent, commercially available	Sadler et al., 2016
	Lions (*Panthera leo*), Kenya/ India	Modified live, multivalent, commercially available. Canarypox-vectoredrecombinant	Kock et al., 1998, Mourya et al., 2019
Cetacean morbillivirus	Whales, dolphins	No current program	
Eastern equine encephalitis virus	Sandhill crane (*Grus canadensis*) and whooping crane	Experimental killed vaccine	Clark et al., 1987
Ebola virus	Chimpanzees	Experimental, virus-like particle	Warfield et al., 2014
Phocine distemper virus	Rare pinnipeds	No current program	

clearly articulated to determine what, if any, action is most appropriate for the disease and species involved. Aims of vaccination may include preventing infection, reducing onward transmission, and reducing disease severity, which may all be important for sustaining viable populations of endangered species and protecting against extinction. Challenges to consider include regulatory requirements and the handling and delivery of vaccines that are safe for target and non-target species and human operators. Knowledge of host biology and ecology is critical in these assessments. Precautionary approaches are always advised, but decisions may have to be made quickly in the face of a die-off, or when cases of a disease in a highly susceptible endangered species are detected.

2.1. Epidemiology and host biology and ecology

Most disease outbreaks of conservation concern occur through spillover transmission of generalist pathogens to small, endangered populations from more abundant reservoir communities (Cleaveland et al., 2007; Cleaveland, 2009). Handling individual rare animals is inherently risky, so interventions targeting reservoir or source populations may be considered more appropriate options. Such interventions may include vaccination of reservoir populations to reduce spillover transmission, removal or separation of sources of infection, or both (e.g. Gilbert et al., 2020). Vaccination of human, companion animal, or livestock reservoirs should be considered and evaluated (Walsh et al., 2017; Kibenge, 2023). For example, in Cambodia, domestic cattle were vaccinated to provide a *cordon sanitaire* against lumpy skin disease around populations of endangered banteng (*Bos javanicus*) and gaur (*B. frontalis gaurus*) (Porco et al., 2023).

A similar approach has been implemented for vaccination of domestic dog (*Canis lupus familiaris*) reservoirs in the Serengeti ecosystem to protect African wild dogs (*Lycaon pictus*) against rabies, with apparent success indicated by the absence of rabies cases in this population since the start of mass domestic dog vaccination (Lembo et al., 2008). However, challenges remain in sustaining large-scale programs in dynamic and highly mobile populations, and a domestic dog vaccination campaign in rural Ethiopia did not prevent a rabies outbreak in Ethiopian wolf populations (Randall et al., 2006). Furthermore, for other generalist pathogens, such as CDV in Africa and Asia, which threaten endangered canids (Canidae) and felids, reservoir systems involve more complex assemblages of domestic and wild carnivores (Viana et al., 2015; Gilbert et al., 2020). With numerous potential wildlife reservoirs, domestic dog vaccination alone is unlikely to safeguard endangered populations, and vaccination of threatened species should be considered (e.g. Gilbert et al., 2020).

Where humans act as the reservoir and source of pathogens for endangered wildlife, which applies to many pathogens that threaten great apes, several other approaches have been implemented. These include public health and One Health programs in neighboring communities (Kalema-Zikusoka and Byonanebye, 2019), guidelines stipulating a minimum distance between human observers and great apes (Macfie and Williamson, 2010), and the introduction of rigorous health screening and face masks for people approaching the animals (Gilardi et al., 2022). The effectiveness of these measures is likely to vary across sites, and the indirect protection provided against specific pathogens is less certain than protection provided by vaccinating individual wild animals themselves.

Another consideration is whether sufficient animals can be vaccinated to achieve the aims of vaccination. In evaluating methods to protect mountain gorillas (*Gorilla beringei beringei*) from Ebola virus, modelling projected that survival rates greater than 50% could be achieved by vaccinating at least half the habituated gorillas within 3 weeks of the first infectious individual (Zimmerman et al., 2023). In considering vaccination of Hawaiian monk seals to protect them against a morbillivirus outbreak, contact network analysis and epidemiological modelling indicated that estimated levels of seal-to-seal contact coupled with the estimated time from vaccination until immunity would be acquired would likely result in morbillivirus “outrunning” the vaccination effort and spreading throughout the population. In contrast, proactive vaccination of 60–85% of the seals at any given sub-population provided

Box 1
Case study of the pre-emptive vaccination of Hawaiian monk seals (HMS) against a morbillivirus epizootic, illustrating the value of long-term population monitoring, stakeholder engagement, and a precautionary approach using sequential implementation to wildlife vaccination programs.

Need

- Protect endangered HMS from a potential morbillivirus epizootic (Baker et al., 2017).
- Species highly susceptible due to low genetic diversity and population-wide seronegativity.

Safety and efficacy

- Required a non-replicative vaccine that could not escape into the wild seal or avian population.
- Safety evaluated sequentially:
  - In a taxonomically similar, non-endangered species (harbor seals) in captivity.
  - In five captive HMS.
  - In seven rehabilitated wild HMS awaiting release.
- Nasal swabs of all vaccinated seals were tested for canarypox DNA to ensure that there would be no risk of poxvirus shedding that could affect non-target avian species.
- Free-ranging HMS were first vaccinated near research facility, allowing regular observations post injection.
- Criteria for vaccination were developed to guide field-based risk assessment:
  - Seals observed for 10 min prior to injection.
  - Injured/unhealthy seals, lactating females and nursing pups avoided.
  - Proximity to nearby wildlife considered.

Feasibility

- Initial targets were seals with high contact rates; any seal that met criteria and was accessible was vaccinated (Baker et al., 2016; Robinson et al., 2018).
- Wild seals always uniquely identified prior to vaccination and observed after injection.
- Efforts expanded to distant islands; protocols adapted to challenges of remote, rugged field camps (vaccine shelf-life, cold-chain and competing priorities).
- Most common complication: pole-syringe needle bending/breakage at hub; no lasting deleterious impacts on individuals or deaths documented.

Stakeholder engagement

- Targeted outreach to local, state, and federal agencies with authorities over other wildlife, human health, and protected areas.
- Targeted outreach to Indigenous cultural liaisons and key conservation entities.
- Engagement of scientific community through workshops and solicitation of advice from subject matter experts.
- Mock vaccination drill implemented in coordination with community conservation partners and highlighted in news and social media.

Opportunities for the future

- Maintain/increase herd immunity: post-weaned pups vaccinated by hand during routine handling for mark-recapture, second injection by pole syringe when asleep on beach.
- By 2023 1029 seals vaccinated (est. 40–60 % sub-population at 7 of 9 subpopulation sites) (Pacific Islands Fisheries Science Center, 2024a, 2024b, 2024c).
- Explore options to examine efficacy and consider booster injections for seals vaccinated in early years of the program.

sufficient herd immunity to control outbreaks if infection were to be introduced (Baker et al., 2016, 2017; Robinson et al., 2018). A preventive vaccination strategy was thus developed to reduce the risk of an outbreak, rather than waiting for detection of morbillivirus-associated mortality to initiate vaccination reactively.

Vaccination strategies are often designed to achieve a critical vaccination threshold that brings the basic reproduction number, R_0, below 1, but to control the disease, lower vaccination coverages may be effective for achieving conservation goals – i.e. reducing the risk of population extinction rather than aiming to control disease per se. Modelling studies of populations such as the Ethiopian wolf, African wild dog and Amur tiger indicate that low-coverage strategies that target a viable minimum 'core' of the population can substantially reduce extinction threats (Haydon et al., 2006; Vial et al., 2006; Gilbert et al., 2020). In some scenarios, vaccination of as few as 10% of individuals was able to protect populations from significant declines. Therefore, vaccination may provide a feasible and effective conservation strategy even in situations where it is logistically or economically challenging to vaccinate a large proportion of the population.

Other aspects of host biology and ecology can also drive decisions to vaccinate. Some endangered species have life stages that are more accessible for injection with minimal stress (e.g. Hawaiian monk seals leave pups alone on beaches after weaning, so the resting pups are accessible), while others have characteristics that allow for consideration of novel approaches (e.g. the grooming behaviour of bats provides opportunities for delivery of oral vaccines). Accessibility and vaccine delivery methods are important factors in determining the feasibility of completing vaccination schedules, such as booster injections.

2.2. Regulatory, social, cultural, and financial considerations

The regulatory frameworks for vaccination of wildlife vary in different countries; thus, local expertise can help ensure successful implementation of a vaccine program. In most countries, different agencies are responsible for endangered species management and vaccine licensing, and other agencies may also be involved if non-target

Box 2
Case study of the potential use of vaccines to prevent the extinction of small populations of Amur tigers due to outbreaks of canine distemper virus (CDV).

Need

- Occupying less than 7 % of their former range, Amur tiger populations are isolated, fragmented and genetically impoverished, increasing their vulnerability to CDV outbreaks.
- In Russia, the first case of CDV in wild Amur tigers was detected in 2003, with further cases in 2010 (Seimon et al., 2013).
- Modelling indicates that CDV increases the extinction likelihood of small populations of 25 Amur tigers by 65 % (Gilbert et al., 2014).
- Wild carnivores are important contributors to the CDV reservoir, indicating that CDV cannot be controlled through vaccination of domestic dogs, therefore vaccination of Amur tigers is the only feasible strategy of controlling CDV impact (Gilbert et al., 2020).

Safety and efficacy

- Modelling found that annual vaccination of 2 Amur tigers per year reduces the 50-yr extinction likelihood of a small population by 2.77 times (Gilbert et al., 2020).
- Vaccination of captive Amur tigers with a modified live vaccine is safe and evokes a measurable humoral response after two doses (Sadler et al., 2016).

Feasibility

- Capture of two tigers each year to deliver a single dose of injectable vaccine costs an estimated $30,000 annually (Gilbert et al., 2020), but without booster, dosing protection cannot be guaranteed.
- Oral or inhalation-based administration of vaccine could represent a more cost-effective means of delivering multiple doses of vaccine (Wimsatt et al., 2003; Du et al., 2022), but obtaining the funding remains challenging.

Stakeholder engagement

- Epidemiological findings and management recommendations have been shared with the research and conservation community through peer-reviewed publications and international meetings in Amur tiger range countries.
- Vaccination of tigers has not been considered within Russia, and the importance of CDV as a threat to tigers has yet to be recognized by national wildlife agencies and professionals.

Opportunities for the future

- Outside Russia, CDV cases and exposure have been detected in Amur tiger populations in India, Nepal, Indonesia and Malaysia (Gilbert et al., 2023), and the only remaining population of Asiatic lions that occurs in Gujarat (Jhala et al., 2019).
- The growing constituency of nations whose populations of big cats are affected by CDV increases the potential for research and production of vaccines.

species could be affected. Regulatory requirements should be addressed early in the planning phase of a project because substantial lead-in times and multiple iterations are often needed to fulfill these requirements, which can vary on a case-by-case, species-specific basis. Most vaccines for endangered wildlife will be commercial products used "off-label," i.e. on a species for which it has not been licensed (e.g. Wilkes, 2023). These products are typically considered safe, but in case of live virus vaccines, careful consideration needs to be given to non-target species at potential risk of exposure to the vaccine. For example, on the Galápagos Islands, where there are no wild canids, vaccinating domestic dogs against CDV with a modified live CDV virus would be preferred over a recombinant canarypox vaccine which could potentially cause disease in endangered birds on the islands (Wilkes, 2023). Because of a similar concern, data on canarypox vaccine shedding from Hawaiian monk seals was generated in controlled settings to inform agencies with oversight of avian wildlife, providing assurance that canarypox shedding was not a threat to those non-target taxa (refer to Box 1).

Enlisting stakeholders and communities early and throughout the process of developing and implementing a vaccination program is crucial to its eventual success (Holm and Kortekaas, 2020). This includes a willingness to provide information, solicit feedback, and revise approaches in response to stakeholder input. For example, the use of genetically modified products, such as recombinant vaccines, has been discouraged in some countries (Dertzbaugh, 1998), which presents challenges to implementation. Anti-vaccination sentiments around some human vaccines exist, as exemplified during the COVID-19 pandemic and in relation to adoption of measles, mumps, rubella (MMR) vaccines (Lane and Gordon, 2024; World Health Organization, 2019), and these sentiments could extend to endangered wildlife (Walsh et al., 2017). Enlisting the early involvement of regulators, stakeholders, and the communities where the vaccine will be implemented can help develop a shared understanding of the rationale for and direction of the vaccination effort.

In some situations, objections to wildlife vaccination have arisen from perceptions regarding the need to differentiate infected from vaccinated animals. Surveillance for domestic animal diseases based on serologic status, like HPAI, do not distinguish between infected and vaccinated animals, and that has implications for international trade if national 'disease-free' status can no longer be demonstrated. Many countries, including the U.S., forbid the import of vaccinated poultry as it might prevent detection of the virus (US Department of Agriculture, Animal and Plant Health Inspection, 2023). Because endangered species are neither traded, nor usually included in national sero-surveillance, the use of certain vaccines for conservation purposes does not conflict with policies to eliminate economically significant pathogens, and trade regulations could be adjusted to emphasize this lack of conflict. For example, vaccination of California condors against HPAI, or saiga antelope (*Saiga tatarica*) against peste des petits ruminants virus (PPRV), could proceed without interfering with surveillance for HPAI in domestic poultry and wild waterfowl, and for PPRV in livestock, respectively.

Wildlife vaccination programs are often funded and implemented by government agencies in response to concerns about public health or livestock economies. For example, the highly successful campaign to

control rabies in wild carnivore reservoirs in the USA using bait-delivered oral rabies vaccine (ORV) was set up to reduce transmission risks to people and domestic animals and has been federally funded through enabling legislation and managed by the U.S. Department of Agriculture, Wildlife Services (Slate et al., 2009). Similarly, vaccination of badgers (*Meles meles*) to reduce transmission of *Mycobacterium bovis* to cattle in the UK has been implemented primarily through government agencies (Department of Environment, Food and Rural Affairs) (Woodroffe et al., 2024), albeit with some funding support through charitable organizations. In comparison, vaccination of endangered species for conservation purposes has not been highly prioritized or legislated by government, with the exception of the USA, where government agencies fund vaccination of black-footed ferrets against plague and CDV (Rocke, 2023) and Hawaiian monk seals against CDV (Robinson et al., 2018) and are developing vaccines for bats against white-nose syndrome (Rocke et al., 2019). Elsewhere, development of endangered species vaccination programs may compete with other conservation initiatives for scarce discretionary funds from non-governmental agencies.

2.3. Vaccine availability, safety and efficacy

Commercially available and novel, target-specific vaccines have been used to manage disease in endangered species, including live-attenuated, virally vectored and protein sub-unit vaccines (Table 1). Vaccine safety and efficacy are primary considerations in assessing potential vaccine use in an endangered species. Because vaccines that are safe in some species may cause disease in others, vaccine safety assessments should be conducted in the target species where possible, using the vaccine of choice and ideally in controlled settings, such as captive facilities. For example, an attenuated canarypox virus vaccine used safely and effectively in canaries and other birds was considered for use in the endangered ʻHawaiʻi amakihi (*Chlorodrepanis virens*), which is threatened by avipoxviruses. However, trials in captive ‘Hawai'i amakihi’ showed the vaccine reverted to virulence and caused disease in some individuals, precluding its use (Atkinson et al., 2012).

If safety trials in target species are not possible, assessments in taxonomically related species may help indicate safety risks to the target species. For example, previous vaccination of harbor seals (*Phoca vitulina*) against CDV provided reassurance that the vaccine would be safe for use in the endangered Hawaiian monk seal (Quinley et al., 2013, Box 1). Similarly, a novel experimental vaccine against avian influenza was tested on black vultures (*Coragyps atratus*) before it was given to endangered California condors (US Fish and Wildlife Service, 2024a). Other approaches draw on recent developments in assessment of human interventions when safety concerns are paramount. For example, vaccines could be administered following principles of stepped wedge trial designs or “first-in-human” protocols (Epidemiology and Modelling of Antibacterial Evasion, 2017) with prescription of the sequence and intervals between administration, intensive monitoring of adverse events, and clear stopping rules that allow for careful assessment of safety.

When possible, including potential sublethal effects (e.g. effects on reproduction or behaviour) in risk assessments of vaccination would help identify other threats to target species. Live vaccines could cause fetal abnormalities or infection of neonates if delivered to pregnant or nursing females. Even without direct effects on the fetus, energetic trade-offs between immune function and other physiologic needs have been shown to lower breeding success (Ilmonen et al., 2000). In female bats, energy demands are greatest in the spring during late pregnancy and lactation, and they can lose their ability to thermoregulate during parturition (Barclay et al., 1980; Wai-Ping and Fenton, 1988). Vaccination at this time could exacerbate their energy requirements, particularly in bats already compromised by white-nose syndrome, like the Northern long-eared bat (*Myotis septentrionalis*), which faces extinction due to the disease (US Fish and Wildlife Service, 2024b). In Hawaiian monk seals given injectable vaccines, behavioral responses to injection were transient, but protocols were developed to safeguard against any potential cumulative impact of repeated disturbance on nearby resting wildlife, with a particular focus on female seals with nursing pups or animals in locations (e.g. rocky cliffs) in which abrupt flight could lead to injury of that individual or other nearby wildlife (Robinson et al., 2018). Finally, risk assessments in non-target species may be required, especially if delivery methods are not species specific. For example, sylvatic plague vaccine, a recombinant raccoonpox virus vectored vaccine expressing plague antigens, was delivered via baits to prairie dogs in grassland ecosystems. Because numerous rodents and other animals could also ingest baits, extensive safety testing was conducted, both in rodent species in captivity and in the field (Tripp et al., 2015; Bron et al., 2018).

Although direct challenge studies are conventionally used to generate data on vaccine efficacy in animals, these trials necessarily require several individuals to succumb to disease (and potentially die) to demonstrate efficacy. Although challenge studies have been carried out for some endangered species (e.g. Rocke et al., 2008; Atkinson et al., 2012), these are rarely acceptable within current social and regulatory frameworks for some species (e.g. black rhinoceros-*Diceros bicornis*; great apes), nor feasible given the number of individuals that might be required to power a study sufficiently to demonstrate efficacy (e.g. Walsh et al., 2017).

In cases where challenge studies are not possible, other correlates of protection could be considered. For example, although black rhinoceros and cheetah (*Acinonyx jubatus*) in the Etosha National Park in Namibia have been vaccinated safely with a commercial anthrax vaccine for over three decades, efficacy of the vaccine at preventing disease was not evaluated directly (Turnbull et al., 2004). Instead, passive transfer of serum from vaccinated animals was shown to confer protection in laboratory mice, suggesting the vaccine does provide protective immunity to both species (Turnbull et al., 2004). Evidence of seroconversion alone is not sufficient to ensure protective efficacy for some vaccines because of the complexity of immune response pathways (Wilkes, 2023) but can provide evidence that the vaccine was successfully delivered. Seroconversion of California condors after vaccination against avian influenza is considered to indicate that the vaccine would reduce severity of disease if these birds were infected with the currently circulating strain of HPAI based on results from previous studies in domestic poultry (US Fish and Wildlife Service, 2024a); however, direct evidence is lacking. Likewise, seroconversion has been used as an indicator of vaccine delivery in Hawaiian monk seals even though the administered vaccine was developed for CDV, and protection from different but related marine morbilliviruses was sought for monk seals (Robinson et al., 2018).

2.4. Feasibility and delivery methods

Methods for delivering vaccines to free-ranging wildlife are often developed hand in hand with vaccine safety and efficacy studies (e.g. Tripp et al., 2014), particularly for novel delivery methods (e.g. oral baits as opposed to injection) because these methods can directly impact safety of target and non-target species (e.g. Bron et al., 2018) and human operators (e.g. Rocke et al., 2004) and the ultimate effectiveness of a vaccination program (e.g., palatability of baits greatly affects uptake and rates of vaccination). Most veterinary vaccines are delivered via injection, which provides a controlled route of delivery but poses considerable challenges for administration to wildlife in comparison with companion animals and livestock. However, the feasibility of injecting vaccines in wildlife may be greater than is often recognized. First, vaccination may be linked with other handling interventions (such as radio-collar fitting/removal, health monitoring, or translocations). For example, black-footed ferrets are routinely captured at some locations annually for health checks and are hand vaccinated against plague and CDV (Rocke, 2023). California condors that have been trained to come to feeders where they can be trapped are currently being vaccinated against HPAI (T. Katzner, USGS, oral communication, 2024). The

rare approachability of some marine mammals (e.g. pinnipeds hauled-out for resting, phocids post-weaning), most Galapagos species, human-habituated great apes, and species in some remote uninhabited areas allow for relatively easy approach, making them amenable to vaccination via injection. For example, a first CDV vaccine is administered to many post-weaning Hawaiian monk seal pups by hand injection during routine handling for mark-recapture studies, and the booster second injection, one month later, is administered by a pole syringe (Jab Stick; Dan-Inject, Austin, TX, USA) when seals are asleep on beaches (Robinson et al., 2018). For some terrestrial mammals, such as African wild dogs, vaccines have also been delivered safely via dart inoculation (Gascoyne et al., 1993). For other species, animals must be trapped or netted, which is labor-intensive, potentially stressful, and carries a risk of injury. However, this approach was successfully implemented for rabies vaccination of Ethiopian wolves, with very few adverse effects and sufficient individuals vaccinated to halt the spread of the rabies outbreak (Knobel et al., 2008).

A hands-off approach may be safer and more desirable for delivering vaccines to endangered species. Oral baits have been used successfully to deliver rabies vaccine to terrestrial carnivores in the US and Europe (Rupprecht et al., 2024) and could be used for endangered species like the Ethiopian wolf (Sillero-Zubiri et al., 2016). For endangered bats (some *Myotis* species), an oro-topical approach is being considered in which bats would be sprayed with a vaccine-laden gel which they ingest while grooming (Rocke et al., 2019). Last, just as aerosol measles vaccines have been given to macaques (de Swart et al., 2006), an aerosol approach could allow vaccination of whales and dolphins against a similar virus, cetacean morbillivirus, by inserting the vaccines into their blowholes using drones that are currently being used for exhaled breath collection (Apprill et al., 2017; Costa et al., 2023). Exploration of novel approaches like these for vaccination of endangered wildlife could help reduce unnecessary handling and stress.

2.5. *Effectiveness - post vaccination monitoring*

The true effectiveness of vaccinating a population of wild animals against a pathogen is necessarily determined in field studies because the conditions that influence vaccine responsiveness under field conditions are typically controlled in captive studies (e.g. sex, age, nutritional and reproductive status, vaccine uptake in the case of bait delivery, and interactions among these variables). The safety and effectiveness of vaccination programs could be assessed using carefully designed post-vaccination monitoring of the target populations and comparisons of survival between vaccinated and unvaccinated individuals, groups, or populations. For example, the positive impact of vaccination of black-footed ferrets against plague was determined by comparing re-encounter rates of vaccinated and unvaccinated individuals as an index of survival in the presence of plague (Matchett et al., 2010). For the Ethiopian wolf, the effectiveness of rabies vaccination in limiting the severity of the outbreak was assessed through modelling (Haydon et al., 2006) which indicated that even low-coverage vaccination may be sufficient to reduce extinction risks while allowing data to be collected from an unvaccinated comparison group. Resource managers may need to contrast vaccine safety and effectiveness against risks of extinction when making decisions about vaccination programs.

3. Opportunities for future vaccine applications

The current HPAI pandemic has already killed tens of thousands of wild mammals and birds (e.g., Southern elephant seals (*Mirounga leonina*), sea lions, seabirds and California condors) and has increased the attention on wildlife vaccination as a conservation tool (Kuiken et al., 2023; Puryear and Runstadler, 2024). Efforts to vaccinate California condors are underway at the time of publication (Kozlov, 2023; US Fish and Wildlife Service, 2024a; World Organization for Animal Health, 2024), and vaccination against HPAI could also be considered for other raptors (Accipitridae), whooping cranes (*Grus americana*), some penguin species. (Roberts et al., 2024), Hawaiian forest birds, monk seals, and other pinnipeds (Spheniscidae) (Gadzhiev et al., 2024a, 2024b), which are among those endangered species threatened by the current pandemic.

For potentially preventable diseases for which vaccines are not currently available (e.g. Table 2), collaborations among the conservation community, vaccinologists, and the pharmaceutical industry could help in the development of new vaccines and the application of new technologies to sustainably manage rare species. For example, marine morbilliviruses are closely related to measles, rinderpest and CDV for which several vaccines have been developed. Marine morbilliviruses could potentially kill thousands of marine mammals, but vaccines against these marine pathogens have not been developed (Van Bressem et al., 2014; Groch et al., 2020). Novel methods of vaccine delivery continue to be developed, improved, and refined. Drones have been employed for dropping baits containing sylvatic plague vaccine for prairie dogs (World Wildlife Fund, 2017) and could be used for animals that are difficult to capture and handle, such as vaccination of whales via their blowholes. The use of transmissible vaccines for wildlife could help prevent transmission of diseases but introduces a new set of risks that must be addressed (Streicker et al., 2024).

Given the range of issues relating to wildlife vaccination, we provide general guidelines for vaccination of wildlife as a starting point for any potential project (Table 3). However, we recommend that scientifically based international guidelines for vaccination of endangered wildlife be developed to facilitate decision making. These guidelines could potentially be developed by the World Organization for Animal Health or the

Table 3
Factors to consider for vaccinating endangered species.

Factors to consider	Examples
Consider life history and ecology of the target species to determine risk tolerances and inform optimal timing of vaccination.	Contact rates estimated from observed association of individual seals on shore were used in models to simulate CDV outbreaks in Hawaiian monk seals. Seasonal haul-out behaviour and life stage of pinnipeds allow easy access for vaccination.
Consult with and adhere to the in-country regulatory framework for importing/using vaccines in field settings.	Regional and national veterinary and agricultural authorities that authorize field trials and manage non-target wildlife.
Engage stakeholders, including the general public, early in project development.	Scientific workshops for local biologists, targeted stakeholder/community outreach, informational public meetings.
Prepare a risk assessment considering all options including the risks of doing nothing.	Environmental Impact Statements under the U.S. National Environmental Policy Act (https://www.epa.gov/nepa/what-national-environmental-policy-act).
Conduct safety and efficacy trials in captive target species if possible, or in taxonomically related species, and assess safety in non-target species if live vaccines are proposed.	Safety assessments of bait-delivered sylvatic plague vaccine conducted in numerous rodent species in captive and field settings.
Determine methods for delivering vaccine to target species, using a hands-off approach if feasible, ensuring safety for target species and operators.	Rabies vaccine delivered to terrestrial carnivores via oral baits. Combination of hand injection and pole syringe to deliver CDV vaccines to Hawaiian monk seals.
Conduct post-treatment monitoring to assess the effectiveness of vaccination in field conditions using correlates of protection when possible and population monitoring.	Survival of bats vaccinated against white-nose syndrome evaluated via radio frequency identification systems, compared to unvaccinated controls.
Disseminate information to international multi-stakeholder groups through forums, reports, and publications.	Presentations to multidisciplinary audiences (e.g., Wildlife Disease Association, World Organization for Animal Health, International Whaling Commission, IUCN Veterinary Specialist Group).

International Union for the Conservation of Nature, like the guidelines established for wildlife translocation and reintroduction (International Union for the Conservation of Nature, Species Survival Commission, 2013).

A forum for transdisciplinary communication and collaboration could help in coordinating vaccination efforts and sharing techniques and experiences, particularly for managing species that cross international borders (e.g., marine mammals, migratory birds). Vaccine developers often may not have insights into the conservation needs or the ecology of wild species of concern. Similarly, veterinarians and wildlife biologists may not be aware of recent advances in vaccinology. Therefore, a multidisciplinary approach that promotes communication and coordination among biologists, government agencies, international organizations dedicated to animal health and welfare, other relevant stakeholders, and the public could help advance the development of tools like vaccination to protect endangered species.

In conclusion, use of wildlife vaccination as a conservation tool has many potential benefits. Implementation of scientifically based approaches and interdisciplinary and transboundary collaborations could help address challenges and concerns regarding vaccinations of rare species. As anthropogenic and environmental stressors interact with disease to constrain many endangered species, vaccination against preventable diseases could help create resilient populations and enable recoveries of negatively affected species.

CRediT authorship contribution statement

Frances M.D. Gulland: Writing – review & editing, Writing – original draft, Conceptualization. **Michelle Barbieri:** Writing – review & editing, Writing – original draft. **Sarah Cleaveland:** Writing – review & editing, Writing – original draft. **Martin Gilbert:** Writing – review & editing, Writing – original draft. **Ailsa J. Hall:** Writing – review & editing, Writing – original draft. **Tonie E. Rocke:** Writing – review & editing, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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