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Review

De-extinction of the Northern white rhinoceros (*Ceratotherium simum cottoni*)

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Abstract. The last survivors of the northern white rhinoceros (NWR, *Ceratotherium simum cottoni*), once widespread across Central and East Africa, are two non-reproductive females under continuous human protection. In order to prevent the extinction of this white rhinoceros subspecies, the *BioRescue* consortium founded in 2019 has developed an innovative reproductive biotechnology program. This holistic rescue strategy implements (*i*) advanced assisted reproductive technologies (aART) including *in vitro* fertilization (IVF) and embryo transfer, (*ii*) stem cell associated techniques (SCAT) for establishing *in vitro* gametogenesis (IVG), and (*iii*) a pangenetic rescue strategy (PRS) that uses the full spectrum of genetic diversity still available by incorporating DNA sequence information from the globally available NWR-museum specimens combined with gene editing to enrich the genetic diversity of the future living population. Key milestones of the BioRescue consortium are: 26 non-surgical oocyte collections in NWR followed by *in-vitro* oocyte maturation and embryo generation, first pregnancy in a southern white rhino (SWR) surrogate after heterologous embryo transfer, establishment of two SWR embryonic stem cell (ESC) lines, NWR induced pluripotent stem cell (iPSC) lines derived from somatic tissue, and robust primordial germ cell-like cell (PGCLC) induction as a first step towards IVG. Beyond biological and technical challenges, an essential part of the *BioRescue* project's operational framework addresses the ethical dimension of this new approach in conservation, ensuring transparency, animal welfare, and societal accountability. This multidisciplinary strategy offers a replicable model in conservation science for rescuing critically endangered or practically extinct species, linking the most advanced reproductive technologies with ethical oversight to safeguard biodiversity.

Key words: Advanced assisted reproductive technologies (aART), Pangenetic rescue strategy (PRS), Stem cell associated techniques (SCAT)

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Introduction

Over the past century, human activities have accelerated species loss to levels comparable with previous mass extinction events. The concept of the “sixth mass extinction” has evolved from a scientific warning into a measurable ecological reality, characterised by rapid decline in planetary biodiversity combined with widespread habitat fragmentation and destruction [1–4]. The prominent threat of extinction to large-bodied, iconic mammals such as all five extant species of the family of *Rhinocerotidae* has been further accelerated by systematic poaching in their natural habitats in Africa and Asia. The western black rhino (*Diceros bicornis longipes*) has recently gone extinct and two of three Asian species are critically endangered [4, 5].

The second largest land mammal after the taxon Elephantidae, the northern white rhinoceros (NWR, *Ceratotherium simum cottoni*), stands as one of the most emblematic examples of functional extinction. Once distributed across Chad, the Central African Republic, Sudan, the Democratic Republic of the Congo, and Uganda, this subspecies of the white rhino has been eradicated in the wild through a fatal combination of poaching and political instability [6–8]. Today, only two subfertile females, the 36 year-old Najin and her 25 year-old daughter Fatu, remain and are protected by 24-h surveillance at Ol Pejeta Conservancy in Kenya. Najin was born to wild-caught parents, Fatu to a wild-caught father and captive-born mother at Dvůr Králové Zoo, and both have been kept at Ol Pejeta Conservancy, Kenya, since 2009. The last NWR male, Sudan, died in 2018, leaving no naturally breeding individuals [9, 10]. However, there are viable cryopreserved spermatozoa from altogether four deceased NWR males (Saut died in 2006; Angalifu and Suni in 2014; Sudan in 2018) which are stored in liquid nitrogen and subjected to strict traceability and quality control.

Conservation strategies for rhinoceroses have traditionally focused on anti-poaching efforts, habitat protection, and translocation programs. These measures were instrumental in restoring populations of the other subspecies of the white rhino, the southern white rhinoceros (SWR, *Ceratotherium simum simum*) in South Africa [11–13] at the beginning of and during the 20th century, raising their numbers from less than 100 to 20.000 in 2012 [14]. However, the northern subspecies presents a remarkable example of a situation in which natural recovery has become biologically impossible without technological intervention.

In 2015, international scientists and conservationists have developed a new holistic conservation strategy for rescuing the NWR employing advanced assisted reproductive technologies (aART) such as oocyte collection (ovum pick-up, OPU), *in vitro* fertilisation (IVF) and embryo transfer, stem cell associated techniques (SCAT) including generation of embryonic (ESCs) and induced pluripotent stem cells (iPSCs) aiming for *in vitro* gametogenesis (IVG) [15]. This approach has recently expanded by aiming at utilizing the full spectrum of NWR genetic information in form of a pangenetic rescue strategy (PRS) which comprises genetic information derived from globally distributed museum and private archive specimens as templates to enrich the genetic diversity of the existing biological material (e.g. tissue of 13 individuals, semen of five individuals, oocytes from one individual, iPSCs of 12 individuals, 38 embryos) [15–19]. This holistic conservation strategy for the critically endangered NWR is shown in Fig. 1.

In October 2025 at the World Conservation Congress, the global conservation community approved this new conservation approach: the annual full assembly voted in favor of employing science-based frameworks for biotechnology in conservation with a majority of 87% of the international union for conservation of nature (IUCN) delegates (IUCN WCC 6th sitting voting results, https://iucncongress2025.org/assembly/vote-results; Annual report Revive & Restore, https://reviverestore.org/annual-reports/annual-report-2025).

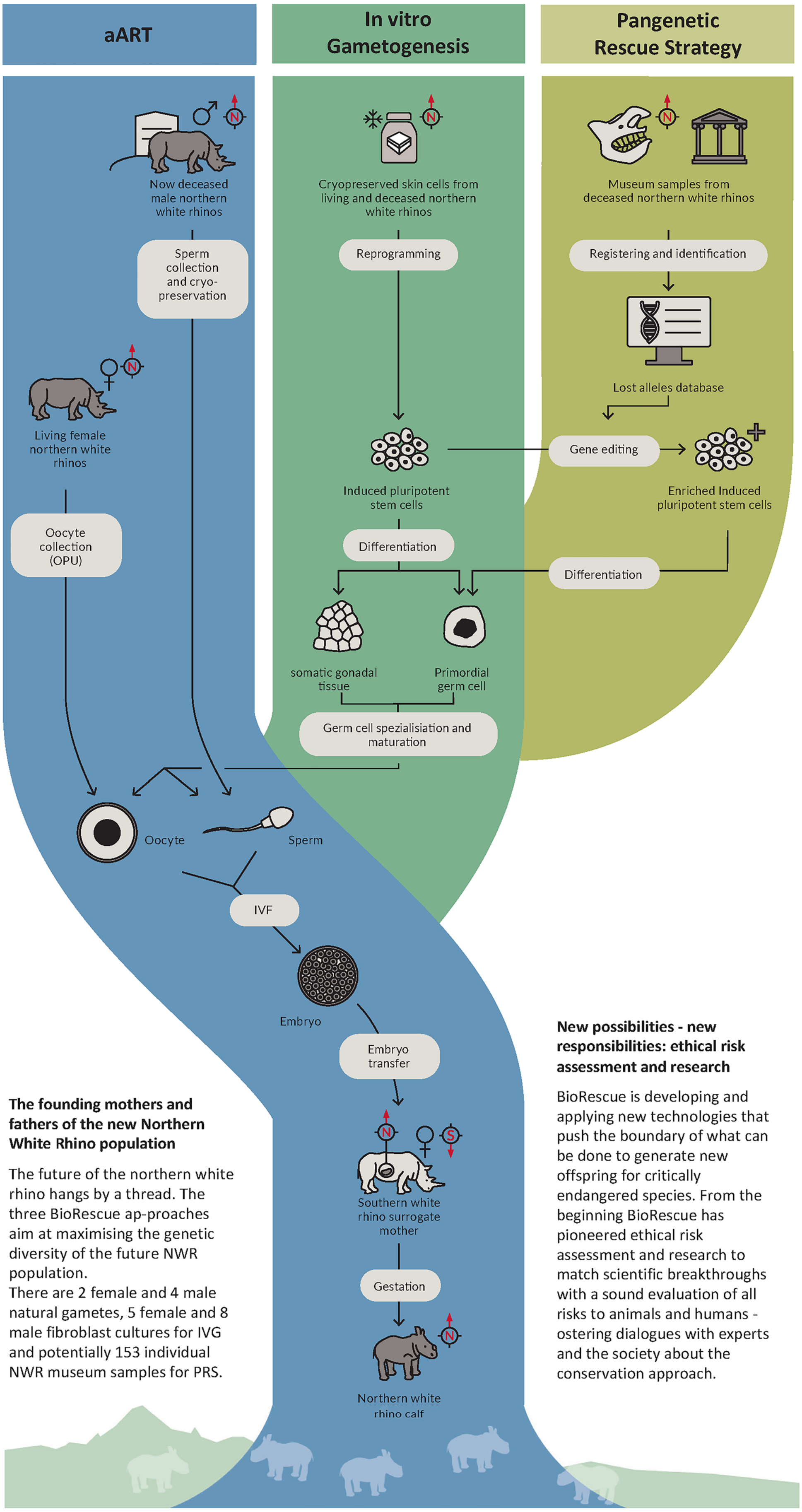
Biobanking, sample collection

The *BioRescue* consortium, coordinated by the German Leibniz Institute for Zoo and Wildlife Research, has developed a new conservation strategy employing biobanking of live wildlife tissue, cells, and gametes as important foundation for cell culture techniques, aART and SCAT [18–21]. This was a joint initiative of several international partners including the Czech Zoo Dvůr Králové (DKZ), the Italian Avantea Foundation, Padua University, Kenya Wildlife Service (KWS), the Kenyan Wildlife Research and Training Institute (WRTI), the US San Diego Zoological Society (SDZS), Singapore Zoo, the Indonesian IPB University and the Leibniz Institute for Zoo and Wildlife Research (IZW). In 2024, the IUCN has created a new species specialist group, the IUCN SSC animal biobanking for conservation specialist group (https://iucn.org/our-union/commissions/group/iucn-ssc-animal-biobanking-conservation-specialist-group). In general, all steps of handling viable wildlife tissue and living cells underlie a strict quality-control process via genomic characterization [22, 23] by deep sequencing of the original material and its products. By applying advanced biotechnologies, these cryopreserved living archives not only contain unique genetic information, but also have the potential to give rise to future living individuals or even entire populations.

aART and iPSC derivation

The NWR BioRescue program started in August 2019. Since then, oocytes have been collected continuously from the two last remaining NWR females, Najin and Fatu, by using a patented OPU system. In total, 26 successful OPU procedures were performed in two females following hormonal stimulation [17, 24]. The females were immobilised by a veterinary anaesthetic team, and transrectal OPU was performed using the specially-designed, needle-guidance system developed for large mammals [17, 24, 25]. The minimally invasive follicular aspiration procedures were conducted under real-time ultrasound guidance to maximise recovery efficiency while avoiding internal bleeding from the surrounding ovarian blood vessels. A total of 308 oocytes were collected which resulted in 38 NWR blastocyst-stage embryos.

Recovered, immature oocytes were transported to the Avantea Laboratory in an optimized holding medium and at constant temperature (22°C) provided by a portable, battery-driven incubator (Micro Q Technologies, USA). Immature cumulus-oocyte-complexes (COC) underwent a modified equine 36 h *in vitro* maturation (IVM) protocol [17, 24]. The matured MII stage oocytes were fertilized with motile sperm selected from thawed cryopreserved samples using intracytoplasmic sperm injection (ICSI) combined with Piezo drilling [17, 24]. To prevent negative inbreeding effects, semen samples of two deceased NWR males, Suni and Angalifu, which had been obtained by electro-ejaculation procedures while still alive, were chosen for the current IVF program [15, 17, 24]. Fertilisation medium and embryo culture conditions were adapted from protocols validated for the domestic horse (*Equus caballus*) and cow (*Bos taurus*) models [26, 27]. Embryos were cultured to the early blastocyst stage and morphologically assessed according to developmental criteria established for the rhinoceros [17, 24]. Out



The founding mothers and fathers of the new Northern White Rhino population

The future of the northern white rhino hangs by a thread. The three BioRescue ap-proaches aim at maximising the genetic diversity of the future NWR population.
There are 2 female and 4 male natural gametes, 5 female and 8 male fibroblast cultures for IVG and potentially 153 individual NWR museum samples for PRS.

New possibilities - new responsibilities: ethical risk assessment and research

BioRescue is developing and applying new technologies that push the boundary of what can be done to generate new offspring for critically endangered species. From the beginning BioRescue has pioneered ethical risk assessment and research to match scientific breakthroughs with a sound evaluation of all risks to animals and humans - ostering dialogues with experts and the society about the conservation approach.

Fig. 1. Three integrated assisted reproductive strategies for the conservation of critically endangered species.

of 308 immature oocytes, 33.4% matured and were injected with a single sperm, 16.6% cleaved, and 12.0% progressed to the blastocyst stage within seven to 13 days post-fertilisation. Embryo morphology was automatically monitored using an advanced embryo culture system with time-lapse technology to continuously assess embryo development (Geri, Genea BIOMEDX, Sydney, Australia), which confirmed rhinoceros embryo viability parameters to be equivalent to those seen in domestic equids [28].

Between 2019 and 2025, a total of 38 NWR embryos were generated, which exclusively derived from Fatu's oocytes. These early blastocyst stage embryos were cryopreserved by a slow freezing protocol and stored in liquid nitrogen (–196°C) for future transfers into SWR surrogates [15, 17, 18, 24]. Sensitive biomaterial such as gametes are stored submerged in liquid nitrogen (–196°C), while more stable biomaterials such as fibroblasts are stored more cost-effectively and cross-contamination-free in nitrogen vapor (–170°C), in accordance with the guidelines of the Ethical Self-Assessment (ETHAS) Biobanking [20] and IUCN Biobanking [29].

Genome-level analyses reveal substantial similarity between the northern and southern white rhinoceros [19, 30–32], supporting the feasibility of xenogenic embryo transfer into SWR surrogate females. Genomic congruencies strengthen the argument that surrogate gestation in SWR females could sustain NWR embryonic development to term.

Fibroblast cultures were established from cryopreserved biopsies (e.g., ear or skin) of two living and eleven already deceased NWR individuals which contain substantial genetic diversity as compared to the SWR [19]. Cells were originally reprogrammed into iPSC using integrating [33] and non-integrating [22, 23, 34] vectors carrying the canonical Yamanaka factors (*OCT4*, *SOX2*, *KLF4*, and *c-MYC*). Maintenance of pluripotency and karyotypic stability over numerous passages demonstrates that reprogramming fidelity can be achieved without genomic integration, reducing the risks of mutation or epigenetic drift. These outcomes echo observations in domestic and wild vertebrates [35–43], consolidating evidence that the Yamanaka-factor system remains universally effective across divergent evolutionary lineages [44].

Derived NWR-iPSC lines were characterized through morphological assessment, immunofluorescence analysis of key pluripotency markers (i.e. OCT4, NANOG, SOX2, and SSEA3), differentiation into cells of the three germ layers, and transcriptome analysis. Gene expression profiles were compared with existing datasets of mammalian pluripotent stem cells, confirming transcriptional signatures consistent with established pluripotent states, such as naïve and primed [22, 45–47]. In addition, two embryonic stem cell lines were derived from four blastocyst-stage SWR embryos [17], which are considered the gold standard for pluripotency, to characterize and qualify iPSC lines and gain a deeper understanding of the optimized reprogramming process.

Long-term genomic stability was monitored through karyotyping [48, 49]. No chromosomal abnormalities or exogenous vector integrations were detected in the final selected iPSC lines [22, 23, 34].

Quality-approved iPSC clones offer the potential to be transformed into primordial germ cell-like cells (PGCLCs) as shown in various species [50–60] for future generation of male and female gametes by establishing efficient IVG protocols [61, 62], enabling restoration of genetic diversity that exceeds the limited pool of cryopreserved gametes currently available in NWR [15–17]. However, except for in the laboratory mouse (*mus musculus* f. domestica) [60, 62], the full cascade from skin-derived fibroblasts to *in vitro*-derived oocytes or spermatozoa (IVG) has not yet been achieved for rhinoceros species. Studies in mouse and human models show that extended culture systems and co-cultivation with somatic gonadal cells are required to complete meiosis [63–65]. Translating these conditions to megafaunal species will demand long-term investment and multi-institutional collaboration.

After establishing a robust IVG protocol for the NWR, this approach will also be employed for the pangenetic rescue strategy to enrich the current living gene pool with genetic information based on the archival DNA samples from globally distributed NWR-museum and private collection specimens (Figs. 1 and 2).

Pangenetic rescue strategy

Museums have been the source of a wealth of information about our natural world, but at the same time they were also historically the reason for the deaths of countless specimens for scientific collections [66–68]. Among those individuals of a species killed for museums or trophy hunting that were included into scientific and private collections, often were individuals of healthy appearance, and of impressive body sizes, large appendixes such as antlers, tusks, or horns, i.e. showing a bias towards high fitness-individuals. This human-caused novel selection pressure in some cases even resulted in morphological changes of the living populations such as the elimination of tusk-bearing males in African elephants [69]. These obvious traits often targeted for trophy hunting are often associated directly or indirectly with further valuable alleles [70] that went missing from the gene pool due to human activity. Identifying these alleles in archival DNA offers the opportunity to enrich the current gene pool with long-lost traits by gene editing.

So far, potentially suitable museum material of at least 153 NWR specimens has been located in seven different countries. Ancient DNA sequencing [71, 72] from historical NWR individuals stored at museums and in private collections will increase our understanding of the genome architecture [19, 30, 31]. It will allow to identify missing alleles which can provide a larger genetic portfolio for enhancing resilience of the future NWR population under changing environmental conditions (resistance to climate change or novel pathogens, e.g. by additional immune gene variants). Target objects for gene editing via CRISPR/Cas9 will be primary fibroblasts and iPSCs [73, 74], whose morphology and chromosomal integrity are closely monitored. The genetically modified material will be used for IVG, embryo generation, and ultimately embryo transfer. This cascade with continuous quality monitoring ensures an ethically responsible approach to avoid genetic deficits of the resulting offspring.

Computed tomography (CT)-based sampling

To obtain optimal historical DNA quality, it is of great importance to select the densest bone regions (most densely ossified regions, MDOR, generally the petrous bones for the skull, and the compacta for long bones) within which the DNA is generally best conserved [75]. CT-scanning allows for identifying and targeting both the optimal sampling site for DNA and the best biopsy access route, causing the least (and least visible) damage to the precious bone material (Fig. 2) [75]. Sampling is performed by sterile drilling (Fig. 2) under clean-room conditions to avoid foreign DNA contamination. The recovered bone powder is used for DNA extraction and sequencing. CT-guided sampling has been shown to improve mean endogenous DNA content, fragment lengths, reduce levels of cytosine deamination and increase absolute numbers of endogenous molecules [76].

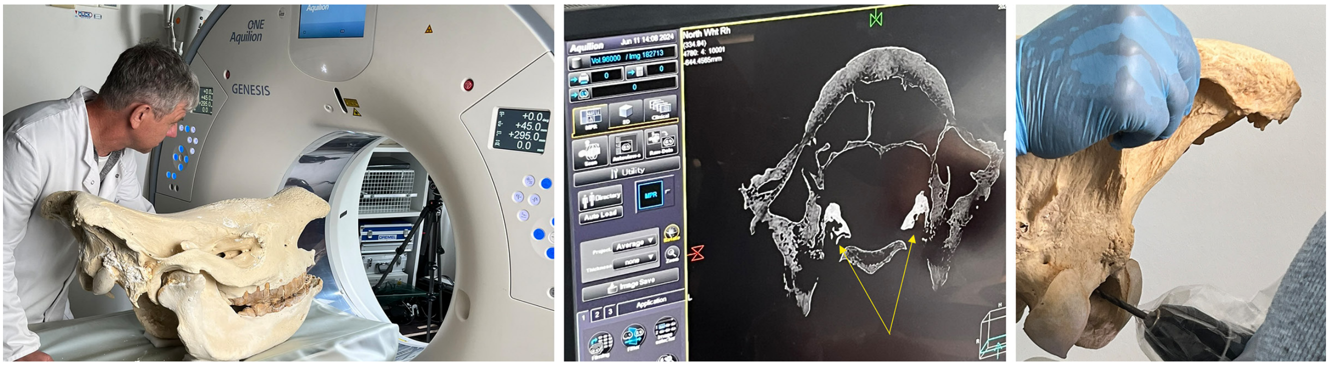


Fig. 2. Computed tomography-based sampling of specimens from museums or private collections helps to target the densest bone structure (most densely ossified region, MDOR, here: *os petrosum*) where DNA is best conserved. This approach has been demonstrated to yield the highest DNA quality. This further allows to choose the least invasive biopsy approach to reach the target bone structure causing minimal destruction, invisible from the outside (here: sterile drilling through the *foramen occipitale magnum*). From bone powder, ancient DNA is extracted and sequenced.

The broader context of megaherbivore rewilding

Beyond the goal of species conservation, re-establishing the ecological function of a self-sustaining wild NWR population carries substantial implications for ecosystem restoration [77]. The NWR represents a keystone megaherbivore and functions as landscape architect, shaping grassland dynamics—for instance, by limiting bushfire propagation through the creation of short-grass corridors, enabling other herbivores that rely on short grass to graze, facilitating nutrient cycling and seed dispersal, and influencing carbon storage [12, 13]. NWR also have an important direct or indirect impact on the endogenous pathogen fauna, with potential zoonotic relevance. Their loss could trigger cascading effects on smaller herbivores, predators, and microbial communities [78].

The successful reintroduction of a genetically healthy, self-sustaining NWR population could restore critical ecological equilibria in Central and East Africa and represent an important contribution to the integrated One Health concept [79]. Currently, the African Parks Board has introduced 16 SWR to Garamba National Park in DRC as a temporary solution to maintain the structure of the habitat. However, the consequences of this ambitious translocation of a neozoon to central Africa remain unclear in terms of their health and survival as well as regarding the impact on microbial and parasitic communities. Collaboration with local conservation agencies and communities will be essential to ensure that technological restoration complements, rather than replaces, habitat protection and anti-poaching measures [6, 9, 10, 14, 80].

From ethical frontiers to governance frameworks

In context of the NWR, the narrative of "the prioritisation of high-cost technological interventions over habitat-based conservation" does not apply as the latter could not save this species while the former can. The rescue of the NWR could not be achieved through conventional conservation techniques and required the development of new conservation tools. In addition, the governmental (BMBF/BMFTR) funding source for this approach was purely directed at biotechnology development and not towards classical conservation per se.

The recent integration of reproductive biotechnology in conservation raises complex ethical questions [81–89]. Concerns include the instrumental use of model animals in experimental protocols such as assessing iPSC clone qualities by the classical teratoma experiment [90], the moral boundaries of interspecies surrogacy, and the prioritisation of high-cost technological interventions over habitat-based conservation. The BioRescue project addresses these challenges through ETHAS framework [20, 85, 86], which systematically evaluates moral justification, animal welfare implications, and societal benefit across each experimental stage from oocyte retrieval to stem cell derivation. This framework has been adapted for cross-disciplinary governance in wildlife research, ensuring transparency and compliance with both institutional and international standards.

Legal foundation

The *BioRescue* program integrates patented reproductive technologies (U.S.: # 10,779,859; Europe: # EP 3369397; ARIPO: # AP/P/2018/010558; Republic of South Africa: # 2018/01416; [25]), stem cell derivation, and innovative ethical assessment tools to develop a comprehensive framework for the pangenetic rescue of the NWR. All experimental designs followed previously established *BioRescue* protocols [17, 22, 24], aligning laboratory procedures with international animal welfare regulations and ethical oversight as defined in the ETHAS framework [20, 85, 86]. All experiments and procedures were performed after receiving all necessary permits that were authorised by KWS, Kenyan WRTI, different European CITES agencies as well as relevant state veterinarian authorities, and were approved by institutional animal care and use committees.

Conclusion

The restoration of the NWR now lies at the intersection of reproductive biotechnology, genomics, and ethical governance. The concept presented here outlines the synthesis of aART, SCAT, PRS, and an ethical framework, leading to a new conservation scheme capable of reversing functional extinction (Fig. 1).

Cryopreserved spermatozoa from long-deceased individuals have retained developmental competence, yielding viable embryos when combined with refined oocyte maturation techniques and IVF techniques [17, 24]. The successful derivation of iPSCs [16, 22, 23, 33, 34] and their partial differentiation into PGCLCs [23] establish the technological foundation for future gamete reconstruction and genetic diversification. Comparative genomic analyses [30–32] confirm that embryonic compatibility between the northern and southern white rhinoceros is biologically feasible, supporting forthcoming embryo transfer initiatives.

The broader implications extend far beyond a single species. By combining technical innovation with ethical self-assessment [20, 81–89], the BioRescue model exemplifies a responsible form of "de-extinction through accountability". It provides a structured pathway by which conservation biotechnology can address moral uncertainty while contributing reproducible knowledge applicable to other endangered taxa. If guided by transparency and precaution, the tools described here may not only rescue the NWR but also redefine how humanity confronts the consequences of biodiversity loss in the Anthropocene.

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