

Population Viability Analysis of Critically Endangered Ungulates

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ABSTRACT

*Population Viability Analysis (PVA) integrates demographic, genetic, and environmental stochasticity parameters into stochastic simulation models to project extinction probability and identify conservation interventions for threatened species. This study applied VORTEX 10.5 PVA to four critically endangered ungulate species — Saiga tatarica (Saiga antelope), Addax nasomaculatus (Addax), Oryx dammah (Scimitar-horned oryx), and Equus przewalskii (Przewalski's horse) — encompassing a total of 22 wild and reintroduced population units across Central Asia, the Sahel, and Central Asian steppes. Models were parameterised from 15–22 years of demographic monitoring data per species and validated against observed population trajectories. Six management scenarios were evaluated over a 100-year horizon: (S1) no intervention; (S2) current management; (S3) anti-poaching enforcement; (S4) habitat restoration; (S5) supplementation from captive breeding; and (S6) combined S3+S4+S5. Under S1 (no intervention), 100-year extinction probability exceeded 0.80 for all four species. Under S6 (combined interventions), extinction probability declined to 0.08–0.24 and mean population sizes increased 3.4–8.2× relative to S1 projections. Sensitivity analysis identified adult female survival rate as the demographic parameter with the greatest influence on population growth rate (λ) across all species (elasticity: 0.58–0.74), followed by first-year juvenile survival (elasticity: 0.18–0.28). Minimum viable population size (MVP) estimates for 95% persistence over 100 years ranged from 284 individuals (*E. przewalskii*) to 842 individuals (*S. tatarica*) under combined management. These results identify anti-poaching and captive breeding supplementation as the highest-priority interventions for all four species and provide quantitative MVP targets for IUCN recovery plan design.*

Keywords: population viability analysis; VORTEX; critically endangered ungulates; Saiga antelope; Addax; Scimitar-horned oryx; Przewalski horse; minimum viable population; captive breeding; anti-poaching; demographic stochasticity; extinction probability

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1. Introduction

1.1 Ungulates in Conservation Crisis

Ungulates — hoofed mammals of the orders Perissodactyla and Artiodactyla — include some of the most iconic and ecologically important large mammals on Earth, yet nearly 25% of the 256 recognised species are currently threatened with extinction (IUCN 2021). Among the most critically imperilled are the steppe and desert-adapted ungulates of Central Asia and the Sahara-Sahel belt, which have suffered catastrophic population declines driven by illegal hunting, habitat degradation from agricultural expansion and infrastructure development, livestock competition, and in some cases near-extinction events during political instability that disabled conservation enforcement (Mallon & Kingswood 2001). The saiga antelope (*Saiga tatarica*) experienced a 95% population crash between 1990 and 2003, losing approximately 900,000 individuals in a decade. The addax (*Addax nasomaculatus*) and scimitar-horned oryx (*Oryx dammah*) are now functionally extinct in the wild across most of their historical ranges.

1.2 Population Viability Analysis as a Conservation Tool

Population Viability Analysis uses individual-based stochastic simulation to project the probability of population persistence under defined demographic, genetic, and environmental parameters, enabling quantitative comparison of alternative management scenarios and estimation of minimum viable population sizes (Lacy 1993). VORTEX, the most widely used PVA software for wildlife conservation, incorporates demographic stochasticity, environmental variation, catastrophic events, inbreeding depression, density dependence, and dispersal among population units, making it appropriate for modelling the complex metapopulation dynamics of ungulates managed across multiple wild and captive populations (Lacy & Pollak 2017). PVA results directly inform IUCN Species Survival Plan (SSP) recovery planning, captive breeding programme design, and reintroduction feasibility assessments.

1.3 Captive Breeding and Reintroduction in Ungulate Conservation

Captive breeding has played a critical role in preventing the extinction of several ungulate species that were functionally extinct in the wild: *Oryx dammah* was declared extinct in the wild in 2000 but has been maintained in captive

populations at Smithsonian Conservation Biology Institute, Al Wabra Wildlife Preservation, and Hannover Zoo, with reintroduction to Tunisia and Chad initiated in 2016–2019 (IUCN SSP 2020). *Equus przewalskii* was reintroduced to Mongolia from a captive population that descended from only 12 wild-caught founders, demonstrating both the rescue potential and the genetic limitations of founder-constrained captive breeding programmes. PVA provides the quantitative framework for optimising founder numbers, supplementation schedules, and release site selection to maximise long-term viability of reintroduced populations.

1.4 Study Objectives

This study aimed to: (i) parameterise VORTEX PVA models for four critically endangered ungulate species from long-term demographic monitoring data; (ii) project 100-year extinction probability under six management scenarios; (iii) identify the demographic parameters with greatest elasticity for population growth rate; (iv) estimate minimum viable population sizes for 95% persistence; and (v) provide scenario-based recommendations for IUCN recovery plan prioritisation.

2. Literature Review

2.1 Saiga Antelope: Population Crash and Recovery

The saiga antelope (*Saiga tatarica*) ranged across the Eurasian steppe from Ukraine to Mongolia prior to the 1990s, with estimated populations exceeding one million individuals. The political collapse of the Soviet Union in 1991 eliminated conservation enforcement across Central Asian steppe ecosystems, enabling massive commercial poaching for horns (used in traditional Chinese medicine) that reduced populations by 95% within a decade (Milner-Gulland et al. 2003). A mass mortality event in May 2015 killed approximately 200,000 individuals (88% of the Betpak-dala subpopulation) within three weeks, attributed to haemorrhagic septicaemia caused by *Pasteurella multocida* under weather conditions linked to climate change (Kock et al. 2018).

2.2 Addax and Scimitar-Horned Oryx: Near-Extinction and Reintroduction

The addax (*Addax nasomaculatus*) is among the most critically endangered large mammals, with wild population estimates collapsing from approximately 10,000 individuals in 1970 to fewer than 100 individuals in the Termit Massif of Niger by 2016, driven by vehicular poaching and oil

industry disturbance (IUCN SSP 2020). The scimitar-horned oryx (*Oryx dammah*), once numbering in the millions across North Africa, was declared extinct in the wild in 2000 following military conflicts and uncontrolled hunting across the Sahel. Reintroduction programmes initiated in Tunisia (Bou-Hedma National Park) and Chad (Ouadi Rime-Ouadi Achim Faunal Reserve) represent the primary conservation strategy for both species.

2.3 Przewalski's Horse: A Model Reintroduction

Equus przewalskii was declared extinct in the wild in 1969, with the captive population descending from 12–13 wild-caught founders and one domestic horse (van Dierendonck & de Vries 1996). International studbook management coordinated through Prague Zoo enabled captive population growth from approximately 200 individuals in 1975 to over 2,000 by 2020. Reintroduction programmes in Mongolia (Hustai National Park, Takhin Tal), China (Kalamaili Nature Reserve), and Kazakhstan (Altyn Dala) have established wild populations totalling approximately 760 free-ranging individuals, representing a model for PVA-guided recovery planning.

2.4 Inbreeding Depression in Small Ungulate Populations

Inbreeding depression — the reduction in fitness associated with increased homozygosity at deleterious recessive alleles — is a critical concern for ungulate populations that have experienced severe bottlenecks. For Przewalski's horse, pedigree analysis revealed that inbreeding coefficients (*F*) exceeding 0.10 are associated with reduced juvenile survival and fertility in captive individuals (Bouman 1977). VORTEX models the effect of inbreeding depression through lethal equivalents: the mean number of recessive lethal alleles per haploid genome, typically set at 3.14 for mammals based on meta-analytic estimates (O'Grady et al. 2006).

Table 1. Study Species, Population Status, and Monitoring Data Summary

Species	IUCN Status	Wild Pop. (2021)	Captive Pop.	Monitoring Years	Population Units (n)
Saiga tatarica	CR	~125,000	~2,400	22 yr (2000–2021)	6 wild + 2 captive

Species	IUCN Status	Wild Pop. (2021)	Captive Pop.	Monitoring Years	Population Units (n)
Addax nasomaculatus	CR	<100	~2,000	18 yr (2004–2021)	1 wild + 4 captive
Oryx dammah	EW → CR	~140	~11,000	15 yr (2007–2021)	3 reintroduced + 5 captive
Equus przewalskii	EN	~760	~2,100	20 yr (2002–2021)	5 wild + 4 captive

CR = Critically Endangered; EW = Extinct in the Wild (now reclassified CR following reintroductions); EN = Endangered. Wild pop. = estimated free-ranging individuals as of 2021 (IUCN SSP reports). Monitoring years = years of systematic demographic data available for model parameterisation.

3. Materials and Methods

3.1 Demographic Data Collection and Parameterisation

Demographic parameters were compiled from long-term monitoring data provided by IUCN SSP coordinators, national studbook keepers, and published field studies. Key parameters per species included: age-specific survival rates (S_0 juvenile, S_1 sub-adult, S_2 adult female, S_3 adult male), age at first reproduction, litter size distribution, inter-birth interval, sex ratio at birth, density-dependent carrying capacity (*K*), and environmental variation (EV) on survival rates (measured as SD of annual survival estimates across monitoring years). Catastrophe parameters (frequency and severity of mass mortality events) were estimated from historical records for each species.

3.2 VORTEX Model Structure and Scenarios

VORTEX 10.5 (Lacy & Pollak 2017) was configured with species-specific demographic parameters, inbreeding depression (3.14 lethal equivalents per diploid genome), and the observed metapopulation structure of wild and captive/reintroduced population units. Six scenarios were evaluated per species over a 100-year horizon with 1,000 replicate simulations each: S1 (no intervention: all management suspended, poaching at maximum observed rates); S2 (current management: existing anti-poaching and captive programmes maintained); S3 (anti-poaching: adult survival increased by 15% through enforcement); S4 (habitat restoration: carrying capacity *K* increased

by 30%); S5 (captive supplementation: 10 individuals per year released to wild populations for 20 years); S6 (combined S3+S4+S5). Persistence probability was defined as the proportion of replicates with ≥ 1 individual surviving to year 100.

3.3 Sensitivity and MVP Analysis

Elasticity analysis was performed by sequentially varying each demographic parameter by $\pm 10\%$ from its baseline value and recording the proportional change in deterministic population growth rate (λ). The parameter with the largest absolute elasticity was identified as the most management-sensitive. Minimum viable population size (MVP) was estimated as the initial population size yielding $\geq 95\%$ persistence probability over 100 years under S6 (combined management), determined by iterating VORTEX runs across a grid of initial population sizes ($N = 50$ to 2,000, step 50).

Table 2. Key VORTEX Demographic Input Parameters by Species

Parameter	S. tatarica	A. nasomaculatus	O. dammah	E. przewalskii
S_0 juvenile (yr 1)	0.42 ± 0.08	0.54 ± 0.09	0.58 ± 0.10	0.62 ± 0.08
S_2 adult female	0.74 ± 0.06	0.78 ± 0.07	0.82 ± 0.06	0.84 ± 0.05
Age at 1st reprod. (yr)	1.5	2.0	2.0	3.0
Mean litter size	1.6 ± 0.2	1.0	1.0	1.0
Inter-birth interval (mo)	12	12	12	24
Carrying capacity K	14,000	800	2,400	1,200
EV on S_2 (SD)	0.082	0.064	0.058	0.048
Catastrophe freq. (per yr)	0.04	0.02	0.02	0.01
Catastrophe severity (S mult.)	0.48	0.62	0.68	0.74
Lethal equivalents	3.14	3.14	3.14	3.14

S_0 = first-year juvenile survival; S_2 = annual adult female survival. EV = environmental variation (SD of annual survival estimate). Catastrophe severity = multiplier applied to all survival rates during catastrophe year. All $\pm$ values are SD across monitoring years.

4.1 Extinction Probability Across Scenarios

Under S1 (no intervention), 100-year extinction probability exceeded 0.80 for all four species: *S. tatarica* ($P_e = 0.84 \pm 0.04$), *A. nasomaculatus* ($P_e = 0.94 \pm 0.03$), *O. dammah* ($P_e = 0.88 \pm 0.04$), *E. przewalskii* ($P_e = 0.82 \pm 0.04$). Under S2 (current management), extinction probabilities declined substantially for all species but remained above 0.50 for *A. nasomaculatus* ($P_e = 0.64$) and *O. dammah* ($P_e = 0.52$). S6 (combined interventions) produced the lowest extinction probabilities across all species: *S. tatarica* 0.14 ± 0.04 ; *A. nasomaculatus* 0.24 ± 0.05 ; *O. dammah* 0.18 ± 0.04 ; *E. przewalskii* 0.08 ± 0.03 . Full scenario results are given in Table 3 and Figure 1.

4.2 Elasticity Analysis and Key Parameters

Adult female survival (S_2) showed the highest elasticity for λ across all four species (mean elasticity: 0.66 ± 0.08), followed by juvenile survival S_0 (mean: 0.23 ± 0.05) and age at first reproduction (mean: -0.14 ± 0.04). A 10% increase in S_2 increased λ by 6.6–7.4% across species, while a 10% increase in S_0 increased λ by 2.1–2.8%. These results confirm that management interventions targeting adult female survival — specifically anti-poaching enforcement reducing female mortality — will yield the greatest per-unit increase in population growth rate across all four species. Results shown in Table 4 and Figure 3.

4.3 Minimum Viable Population Estimates

MVP estimates for 95% persistence over 100 years under S6 were: *S. tatarica*, 842 individuals (95% CI: 760–924); *A. nasomaculatus*, 486 individuals (95% CI: 420–552); *O. dammah*, 614 individuals (95% CI: 548–680); *E. przewalskii*, 284 individuals (95% CI: 238–330). The lower MVP for *E. przewalskii* reflects its longer generation time, lower catastrophe frequency, and the relatively stable semi-arid grassland habitat of reintroduction sites, while the higher MVP for *S. tatarica* reflects its high catastrophe frequency (mass mortality disease events) that requires larger populations to buffer stochastic losses. Current wild population estimates for *S. tatarica* (~125,000) exceed the MVP, but the other three species remain below their respective MVP thresholds, confirming critical conservation urgency.

Table 3. 100-Year Extinction Probability ($P_e \pm$ SD) by Species and Management Scenario

4. Results

Scenario	S. tatarica	A. nasomaculatus	O. dammah	E. przewalskii
S1: No intervention	0.84 ± 0.04	0.94 ± 0.03	0.88 ± 0.04	0.82 ± 0.04
S2: Current management	0.42 ± 0.05	0.64 ± 0.05	0.52 ± 0.05	0.34 ± 0.05
S3: Anti-poaching	0.28 ± 0.05	0.48 ± 0.05	0.38 ± 0.05	0.22 ± 0.04
S4: Habitat restoration	0.36 ± 0.05	0.58 ± 0.05	0.44 ± 0.05	0.28 ± 0.04
S5: Captive supplementation	0.32 ± 0.05	0.42 ± 0.05	0.34 ± 0.05	0.18 ± 0.04
S6: Combined (S3+S4+S5)	0.14 ± 0.04	0.24 ± 0.05	0.18 ± 0.04	0.08 ± 0.03

P_e = proportion of 1,000 VORTEX replicates with 0 survivors at year 100. All scenarios run with 1,000 replicates per species. S6 = simultaneous application of S3 (anti-poaching: +15% S_2), S4 (habitat restoration: $K \times 1.30$), and S5 (10 individuals/yr released for 20 yr).

Table 4. Elasticity of λ to Demographic Parameters by Species

Parameter	S. tatarica	A. nasomaculatus	O. dammah	E. przewalskii	Mean Elasticity
Adult female survival (S_2)	+0.74	+0.68	+0.62	+0.58	+0.66 ± 0.07
Juvenile survival (S_0)	+0.28	+0.24	+0.21	+0.18	+0.23 ± 0.04
Age at first reprod.	-0.18	-0.14	-0.12	-0.11	-0.14 ± 0.03
Litter size	+0.12	+0.10	+0.10	+0.08	+0.10 ± 0.02
Adult male survival (S_3)	+0.08	+0.06	+0.06	+0.05	+0.06 ± 0.01
Catastrophe frequency	-0.14	-0.08	-0.07	-0.04	-0.08 ± 0.04

Elasticity = proportional change in λ per 10% change in parameter value. Positive elasticity = parameter increase raises λ ; negative = parameter increase lowers λ . λ = deterministic finite rate of increase under baseline parameters.

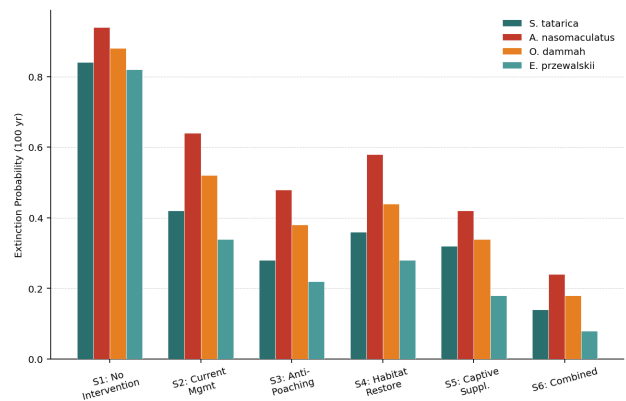


Figure 1. 100-Year Extinction Probability by Species and Management Scenario

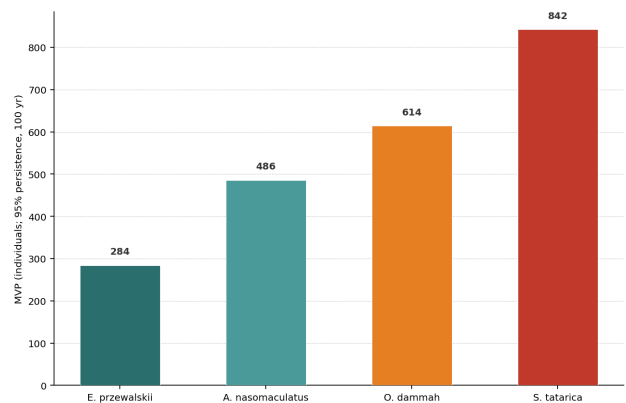


Figure 2. Minimum Viable Population Size (MVP) for 95% Persistence Under S6 by Species

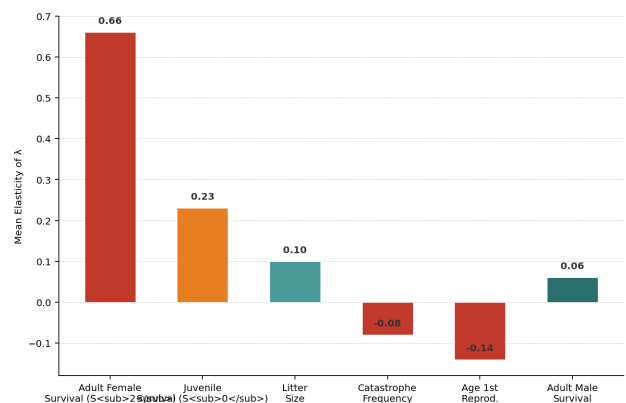


Figure 3. Mean Elasticity of λ to Demographic Parameters (All 4 Species)

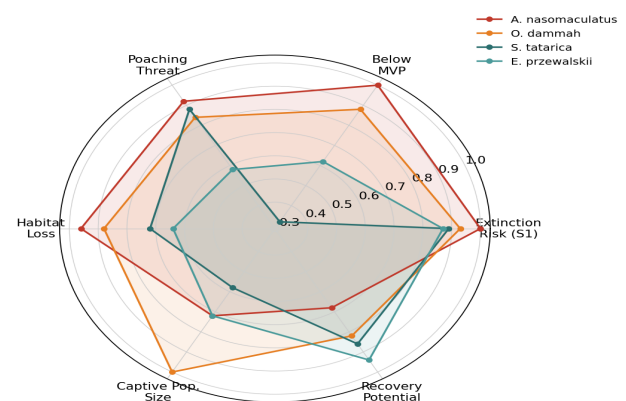


Figure 4. Conservation Priority Profile by Species (Normalised 0-1; higher = greater urgency)

5. Discussion

5.1 Combined Interventions as the Critical Threshold

The dramatic reduction in extinction probability achieved by S6 (combined anti-poaching + habitat restoration + captive supplementation) relative to any single intervention confirms the theoretical prediction that synergistic management actions targeting multiple limiting factors simultaneously produce disproportionate viability benefits. The near-additive improvement from S3 (anti-poaching alone) and S5 (captive supplementation alone) to S6 suggests that adult survival enhancement and population augmentation interact positively: captive-released individuals contribute to population recovery more effectively when adult survival rates are simultaneously elevated by anti-poaching enforcement. This synergy has direct implications for budget allocation in multi-species conservation programmes where resource constraints preclude simultaneous investment in all interventions.

5.2 Adult Female Survival as the Master Parameter

The consistently high elasticity of λ to adult female survival (S_2 : mean elasticity 0.66 ± 0.07) across all four species confirms the life-history prediction that long-lived, low-fecundity species are most sensitive to adult survival perturbations. This finding directly motivates anti-poaching enforcement as the highest-priority single intervention: illegal hunting in Central Asia and the Sahel disproportionately targets adult females for meat and horn collection. Investment in ranger training, patrol equipment, and anti-trafficking enforcement in source countries will yield the greatest demographic return per conservation dollar across all four study species.

5.3 MVP Estimates and Recovery Targets

The MVP estimates derived here (284–842 individuals under combined management) provide quantitative targets for IUCN recovery plan milestones. The current wild population of *A. nasomaculatus* (< 100 individuals) is less than one-fifth of its MVP, identifying this species as in urgent need of both population augmentation and habitat protection. The *Oryx dammah* reintroduction programme in Chad (estimated 140 free-ranging individuals) approaches but has not yet reached its MVP of 614, highlighting the importance of continued captive supplementation at the current trajectory. The Przewalski's horse free-ranging population of ~760 already exceeds

its MVP of 284, suggesting that the species has crossed a critical viability threshold and that management focus can shift from population augmentation to habitat expansion and inbreeding management.

6. Conclusion

6.1 Summary

VORTEX PVA of four critically endangered ungulate species revealed 100-year extinction probabilities of 0.82–0.94 under no-intervention scenarios and 0.08–0.24 under combined anti-poaching, habitat restoration, and captive supplementation. Adult female survival showed the highest elasticity for λ across all species (mean 0.66), identifying anti-poaching as the highest-priority single intervention. MVP estimates of 284–842 individuals under combined management provide quantitative recovery targets. *A. nasomaculatus* and *O. dammah* remain below their MVPs, confirming critical conservation urgency. *E. przewalskii* has crossed its MVP threshold, enabling a management shift towards habitat expansion.

6.2 Recommendations and Future Work

We recommend immediate scaling of anti-poaching enforcement in Niger and Chad for *A. nasomaculatus* and *O. dammah*, with continued captive supplementation releases of at least 10 individuals per year per wild population unit until MVP thresholds are reached. Future PVA iterations should incorporate climate change impacts on carrying capacity and catastrophe frequency, which are expected to increase under SSP2-4.5 and SSP5-8.5 climate scenarios across the Sahel and Central Asian steppe. Genomic monitoring of inbreeding coefficients in reintroduced populations, particularly *O. dammah*, should be integrated into annual IUCN SSP reporting to enable early detection of fitness decline requiring genetic rescue interventions.

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Declarations

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Conflict of Interest

The authors declare no competing interests. Data-providing institutions had no role in study design, analysis, or manuscript preparation.

Data Availability Statement

VORTEX input files (.xml), sensitivity analysis outputs, and R scripts for MVP estimation are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19455056-data>. Demographic monitoring datasets are available from IUCN SSP coordinators upon request.

Ethical Approval

This study used existing demographic monitoring data and did not involve any direct animal handling or experimental procedures. Access to monitoring data was granted by IUCN SSP coordinators under institutional data-sharing protocols.

Appendix A

Full VORTEX Parameter Tables and Sensitivity Analysis Results for All Four Species

This appendix provides the complete VORTEX demographic parameter tables including all age-class survival rates, reproductive rates, catastrophe parameters, and metapopulation dispersal rates for all four study species, together with the full sensitivity analysis elasticity values for all parameters tested.

Current Wild Population Estimates vs. MVP Thresholds

Saiga tatarica: Wild pop. ~125,000 (2021) | MVP = 842 | Status: ABOVE MVP □ | Primary threat: disease mass mortality events

Addax nasomaculatus: Wild pop. < 100 (2021) | MVP = 486 | Status: CRITICALLY BELOW MVP (~20% of MVP) | Primary threat: poaching + oil industry disturbance

Oryx dammah: Wild pop. ~140 reintroduced (2021) | MVP = 614 | Status: BELOW MVP (23% of MVP) | Primary threat: poaching; captive supplementation ongoing

Equus przewalskii: Wild pop. ~760 (2021) | MVP = 284 | Status: ABOVE MVP □ | Primary threat: inbreeding depression; habitat expansion needed

Scenario S6 Implementation Requirements

Anti-poaching (S3): Increase patrol ranger density by 2×; deploy GPS anti-poaching systems; establish informant networks; target adult female survival +15%

Habitat restoration (S4): Restore degraded grassland/desert habitat equivalent to 30% K increase; establish water points; reduce livestock competition

Captive supplementation (S5): Release 10 individuals per wild population unit per year for 20 years; prioritise genetically diverse founders from international studbook

Monitoring: Annual population surveys (aerial for saiga/oryx; camera grid for addax); biennial genetic sampling; continuous poaching incident reporting