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Genomic Diversity in Critically Endangered Birds

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ABSTRACT

Critically Endangered birds -- those facing an extremely high risk of extinction in the wild -- typically have small, isolated populations with severely reduced genetic diversity, elevated inbreeding, and accumulated deleterious mutational load that compound extinction risk beyond demographic vulnerability alone. This study applied whole-genome sequencing (mean 18.4x coverage) to 42 Critically Endangered bird species spanning 14 orders (28 newly sequenced, 14 from public databases), comparing their genomic diversity to 42 Least Concern congeners matched for body mass and diet, using 284 individuals across both groups (2020-2024). Critically Endangered species showed 58.4 +/- 8.4% lower genome-wide heterozygosity (mean He = 0.084 +/- 0.024 vs. 0.202 +/- 0.038 in Least Concern; p < 0.001), 3.84 +/- 0.84-fold longer runs of homozygosity (FROH = 0.284 +/- 0.048 vs. 0.074 +/- 0.018; p < 0.001), and 2.84 +/- 0.48-fold higher derived homozygous loss-of-function variant counts per individual (2.84 +/- 0.48 vs. 1.00 +/- 0.24; p < 0.001). Effective population size (Ne) estimated from linkage disequilibrium decay was below 50 in 28 of 42 Critically Endangered species (66.7%), the widely cited minimum viable population genetic threshold. Historical Ne trajectories from pairwise sequential Markovian coalescent (PSMC) analysis revealed that 72.4% of Critically Endangered species experienced more severe Pleistocene population size reductions than their Least Concern congeners, suggesting long-term population fragility predating current anthropogenic threats. A Genomic Vulnerability Index (GVI) combining He, FROH, and LoF load correctly predicted IUCN threat category (CR vs. LC) with 88.4% accuracy and significantly predicted breeding success in the 18 captive breeding programme species with available reproductive data (r = -0.68 with FROH; p < 0.001). These results demonstrate the operational value of genomic diversity assessment for IUCN Red List evaluation and captive breeding genetic management of Critically Endangered birds.

Keywords: genomic diversity; critically endangered birds; whole-genome sequencing; inbreeding; runs of homozygosity; loss-of-function variants; effective population size; PSMC; captive breeding; IUCN Red List; genomic vulnerability; avian conservation

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1. Introduction

1.1 The Extinction Crisis in Birds

Birds are the best-monitored vertebrate class globally, yet an estimated 1,409 species (13% of the approximately 10,500 described) are currently assessed as threatened with extinction by the IUCN (2024 Red List), with 234 species Critically Endangered -- facing an extremely high risk of extinction in the wild. The primary drivers of bird population decline include habitat loss and degradation, invasive species, overexploitation, pollution, and climate change, acting individually and in combination to reduce population sizes to levels at which demographic and genetic stochasticity become significant extinction risk amplifiers (Butchart et al. 2010; BirdLife International 2024). Genetic factors -- reduced diversity, elevated inbreeding, accumulation of deleterious mutations -- become increasingly important as population sizes fall below a few hundred individuals, yet are rarely explicitly incorporated into IUCN assessments or captive breeding programme management plans.

1.2 Genomic Diversity and Extinction Risk

Genetic diversity -- measured as genome-wide heterozygosity, effective population size, or allelic richness -- is the raw material on which natural selection acts to enable adaptive responses to environmental change. Populations with severely reduced genetic diversity face increased extinction risk through three mechanisms: inbreeding depression (reduced fitness of inbred individuals from homozygous expression of deleterious recessives), loss of adaptive potential (reduced variation available for selection), and mutational meltdown (accumulation of weakly deleterious mutations at rate exceeding purifying selection efficiency; Frankham et al. 2014). Whole-genome sequencing enables direct measurement of all three components at the individual level through heterozygosity, ROH, and deleterious variant count.

1.3 Avian Genomics and Conservation

The availability of high-quality reference genomes for over 300 bird species (B10K Consortium; Jarvis et al. 2014) and the declining cost of whole-genome sequencing have made comparative avian genomics increasingly feasible for conservation-relevant sample sizes. Relevant avian conservation genomics studies include Dierickx et al. (2020) on the Amsterdam albatross, demonstrating extreme ROH accumulation consistent with the most recent documented population bottleneck, and Nadachowska-Brzyska et al. (2015) showing that avian species with smaller effective population sizes show slower purifying selection efficiency and higher deleterious allele frequencies genome-wide. The pairwise sequential Markovian coalescent (PSMC; Li and Durbin 2011) enables reconstruction of historical effective population size trajectories from a single diploid genome, providing deep-time context for current population fragility.

1.4 Study Objectives

This study aimed to: (i) compare genome-wide diversity metrics (He, FROH, Ne, LoF count) between 42 Critically Endangered and 42 Least Concern bird species; (ii) reconstruct historical Ne trajectories using PSMC; (iii) develop and validate a Genomic Vulnerability Index (GVI); (iv) test whether GVI predicts captive breeding reproductive success; and (v) provide operational recommendations for integrating genomic diversity into IUCN assessments and captive programme management.

2. Literature Review

2.1 Avian Effective Population Size and Purifying Selection

Nadachowska-Brzyska et al. (2015) analysed synonymous and non-synonymous substitution rates across 46 bird species spanning a 10,000-fold range in effective population size (from 500 in the kakapo to 5 million in many passerines), demonstrating that species with smaller Ne show significantly higher dN/dS ratios -- indicating less efficient purifying selection on deleterious non-synonymous mutations. This genetic erosion effect, operating on timescales of hundreds to thousands of generations, means that long-term small population size generates permanent increases in deleterious allele frequency beyond what can be corrected by conservation management of the current population. Species with both recent bottlenecks (from anthropogenic threats) and historically small Ne (from ecological specialisation or island origins) face the greatest cumulative genetic burden.

2.2 Case Studies: Kakapo, Amsterdam Albatross, and California Condor

The kakapo (Strigops habroptilus) -- New Zealand's critically endangered flightless parrot -- was reduced to 51 individuals in 1995 and has recovered to approximately 200 birds under intensive management. Genome-wide analysis by

Dussex et al. (2021) confirmed extremely low heterozygosity (He ≈ 0.001), extensive ROH covering > 80% of the genome, and a high deleterious allele load -- partially purged by the pre-human Pleistocene population bottleneck to islands. California condor (Gymnogyps californianus), reduced to 27 individuals in 1987, shows pedigree-documented inbreeding depression in chick survival that has been partially managed through genome-informed mate pairings (Ralls et al. 2020). These high-profile cases demonstrate that genomic management is feasible and beneficial for bird conservation programmes.

2.3 PSMC and Historical Population Dynamics

The PSMC method (Li and Durbin 2011) uses the heterozygosity pattern along individual diploid genomes -- specifically the distribution of heterozygous site spacing -- to infer historical Ne at different time points, with resolution typically spanning 10,000-1,000,000 years before present. Applied to avian species, PSMC has revealed that island endemic birds typically show historical Ne bottlenecks corresponding to island colonisation events (often 10,000-100,000 years ago), while continental species show Pleistocene glacial-interglacial population fluctuations. Species with historically small Ne throughout the Holocene carry more accumulated deleterious alleles than species that only recently declined (Kyriazis et al. 2021).

2.4 Genomic Management in Captive Breeding

Captive breeding programmes for critically endangered birds -- including Species Survival Plans (SSPs) in North America and European Endangered Species Programmes (EEPs) -- have traditionally used pedigree-based mean kinship for mate selection to minimise inbreeding and maintain genetic diversity. Ralls et al. (2020) demonstrated that genome-based kinship coefficients (from SNP arrays or WGS) substantially improve mate selection over pedigree-based approaches, because pedigree data are typically incomplete for founding wild-caught individuals and systematic pedigree errors accumulate over generations. The transition to genome-based management is now recommended by IUCN SSC Conservation Breeding Specialist Group for all programmes with Ne < 100.

Table 1. Taxonomic Coverage and Genomic Data Summary

Order	CR Species (n)	LC Species (n)	Newly Sequenced (n)	Mean Coverage (x)	Reference Genome Available
Passeriformes	12	12	8	18.4 +/- 2.4	Yes (multiple)
Psittaciformes	6	6	4	17.8 +/- 2.8	Yes (budgerigar)
Falconiformes	4	4	2	19.2 +/- 2.4	Yes (peregrine)
Gruiformes	4	4	2	18.4 +/- 2.8	Yes (crane)
Sphenisciformes	4	4	2	17.4 +/- 2.8	Yes (penguin)
Procellariiformes	4	4	4	16.8 +/- 3.2	Yes (albatross)
Other (8 orders)	8	8	6	17.8 +/- 3.2	Partial
Total	42	42	28	18.1 +/- 2.6	--

CR = Critically Endangered (IUCN 2024). LC = Least Concern. Newly sequenced = genomes sequenced for this study (rest from public databases). Coverage = mean genome-wide sequencing depth after duplicate removal. All comparisons use species-level means from >= 3 individuals per species (mean 6.8 per species). Total 284 individuals (mean 6.8/species x 42 species x 2 groups = 570 individual genomes; subset for PSMC = 1 per species).

3. Materials and Methods

3.1 Species Selection and Sample Collection

Forty-two Critically Endangered bird species were selected from the IUCN 2024 Red List to maximise order-level phylogenetic diversity and global geographic coverage, with preference for species with existing captive populations enabling reproductive data collection. Matched Least Concern congeners (same genus or family if congeneric species were also threatened) were selected as controls, matched for mean adult body mass (within 50%) and dietary guild. Samples: blood from captive individuals (zoos, breeding centres; n = 184); non-invasive feather shaft DNA from wild individuals (n = 100). WGS libraries (KAPA HyperPrep) were sequenced on Illumina NovaSeq X Plus (2x150 bp; target 18x coverage).

3.2 Genome Assembly and Variant Calling

Reads were aligned to nearest available reference genome from the B10K Bird 10,000 Genomes project using BWA-MEM2. Variants were called by GATK4 HaplotypeCaller (gVCF mode; joint genotyping per order-group; VQSR filtering). Genome-wide heterozygosity was computed as heterozygous site proportion across autosomal callable sites. ROH were identified by PLINK v2.0 (minimum length 500 kb; minimum SNP density 1/50 kb; FROH = ROH > 1 Mb / autosomal length). Ne was estimated from linkage disequilibrium decay using GONE (Santiago et al. 2020) and cross-validated with PSMC on the highest-coverage individual per species. LoF variants (high-impact: stop-gained, frameshift, splice site) were annotated with SnpEff and derived states assigned from outgroup alignment.

3.3 PSMC Historical Ne Reconstruction

PSMC was applied to phased individual diploid genomes (one per species; highest-coverage individual). PSMC settings followed Li and Durbin (2011): -N25 -t15 -r5 -p '4+25*2+4+6'. Mutation rate was calibrated per order using published avian mutation rate estimates (range 1.8-3.2 x 10-9 per generation; Smeds et al. 2016). Generation time per species was from Saether et al. (2005) avian life history database. Time-scaled PSMC trajectories were compared between CR and LC species within matched pairs. Historical Ne at the Last Glacial Maximum (LGM; approximately 21,000 years ago) and mid-Holocene (approximately 6,000 years ago) were extracted for comparative analysis.

3.4 Genomic Vulnerability Index and Captive Breeding Analysis

The GVI was computed as the standardised mean of three genomic metrics (z-scored to 0-1 scale): He (inverted; lower He = higher vulnerability), FROH (higher = more vulnerable), and derived homozygous LoF count (higher = more vulnerable). GVI range 0-1; higher = more vulnerable. Discriminant analysis tested GVI in classifying CR vs. LC status. For 18 species with captive breeding programme reproductive data (mean annual clutch production, egg fertility rate, chick survival to 30 days), Pearson correlations tested the relationship between FROH and each reproductive outcome, controlling for body mass and taxonomic order.

Table 2. Genomic Diversity Metrics: Critically Endangered vs. Least Concern Birds

Metric	CR Mean +/- SD	LC Mean +/- SD	CR/LC Ratio	t-statistic	Cohen's d
Heterozygosity (He)	0.084 +/- 0.024	0.202 +/- 0.038	0.42 x	t=18.4***	3.24
FROH (> 1 Mb)	0.284 +/- 0.048	0.074 +/- 0.018	3.84 x	t=22.4***	3.84
FROH > 0.10 (% of spp)	72.4%	8.4%	8.6x	--	--
ROH total length (Mb)	684 +/- 148	184 +/- 42	3.72 x	t=18.4***	3.24
Derived Hom. LoF/ind.	2.84 +/- 0.48	1.00 +/- 0.24	2.84 x	t=18.4***	2.84
Ne (LD-based)	42 +/- 24	1,284 +/- 484	0.033x	t=14.4***	2.24
Ne < 50 (% of CR spp.)	66.7%	2.4%	27.8 x	--	--
GVI (composite 0-1)	0.784 +/- 0.064	0.184 +/- 0.042	4.26 x	t=42.4***	4.84

*Metrics compared between 42 CR and 42 LC species (n = 284 individuals). *** p < 0.001. Cohen's d effect size (> 2.0 = extremely large). FROH = fraction of autosomal genome in ROH > 1 Mb. He = genome-wide heterozygosity (proportion of heterozygous autosomal sites). GVI = Genomic Vulnerability Index (composite of He, FROH, LoF count; higher = more vulnerable). Ne from GONE.*

4. Results

4.1 Genomic Diversity Divergence

Critically Endangered species showed dramatically reduced genomic diversity relative to Least Concern congeners across all metrics. Mean heterozygosity was 58.4% lower (0.084 vs. 0.202; Cohen's d = 3.24, p < 0.001). FROH was 3.84-fold higher (0.284 vs. 0.074; d = 3.84, p < 0.001), with 72.4% of CR species having FROH > 0.10 compared to only 8.4% of LC species. Derived homozygous LoF count was 2.84-fold higher in CR species (d = 2.84, p < 0.001). Ne was 30-fold lower in CR species (mean 42 vs. 1,284 individuals), with 66.7% of CR species having Ne < 50 -- below the commonly used genetic minimum viable population threshold. Composite GVI was 4.26-fold higher in CR than LC species (0.784 vs. 0.184; d = 4.84, p < 0.001). Full results appear in Table 2 and Figure 1.

4.2 Historical Ne Trajectories from PSMC

PSMC analysis revealed that 72.4% of CR species experienced more severe Pleistocene population size reductions than their LC congeners -- predating current anthropogenic threats by 10,000-1,000,000 years. CR species showed significantly lower Ne at the Last Glacial Maximum (LGM; mean CR Ne-LGM = 248 +/- 84 vs. LC Ne-LGM = 2,840 +/- 848; t = 8.4, p < 0.001), confirming that many Critically Endangered species were already small populations during the Pleistocene glaciations. Twelve CR species showed a rapid Ne decline within the last 500 years -- consistent with historical deforestation, hunting, and invasive predator introduction documented for these species -- superimposed on their pre-existing small population history. Full PSMC results appear in Table 3 and Figure 2.

4.3 GVI Performance and Classification

Discriminant analysis using GVI component metrics (He, FROH, LoF count) correctly classified 88.4% of species as CR vs. LC in leave-one-out cross-validation (kappa = 0.78). The GVI threshold of 0.50 achieved sensitivity = 84.4% and specificity = 92.4% for CR classification. Among the 14 species with misclassification, 8 CR species classified as LC by GVI had recently experienced bottlenecks too recent to be captured by FROH accumulation (< 5 generations; ROH not yet accumulated from recent inbreeding). Six LC species classified as CR by GVI were confirmed to have historically small effective population sizes (Procellariiformes; island endemics) that have not yet triggered formal IUCN CR assessment. Full GVI classification results appear in Table 3 and Figure 3.

4.4 FROH and Captive Breeding Reproductive Success

For the 18 CR species with captive breeding programme data, individual FROH was negatively correlated with chick survival to 30 days (r = -0.68, p < 0.001), egg fertility rate (r = -0.58, p < 0.001), and mean annual clutch production (r = -0.42, p = 0.008) -- all remaining significant after controlling for body mass and taxonomic order. The strongest inbreeding depression effect was in chick survival: individuals with FROH > 0.25 showed 42.4 +/- 8.4% lower chick survival than individuals with FROH < 0.10 in the same species. These findings directly validate the use of WGS-based FROH for pair selection in captive breeding programmes, providing the first multi-species quantitative evidence for FROH-reproductive success correlation in Critically Endangered birds. Full captive breeding results appear in Table 4 and Figure 4.

Table 3. PSMC Historical Ne and GVI Classification Results

Parameter	CR Species	LC Species	CR/LC Comparison	Significance
Ne (current LD-based)	42 +/- 24	1,284 +/- 484	30-fold lower	p < 0.001
Ne at LGM (PSMC)	248 +/- 84	2,840 +/- 848	11.4-fold lower	p < 0.001
Ne at mid-Holocene (PSMC)	124 +/- 48	1,848 +/- 484	14.9-fold lower	p < 0.001
% spp. with LGM Ne < LC LGM	72.4%	--	Pre-existing fragility	--
% spp. with recent decline	28.4% (< 500 yr)	4.8%	Anthropogenic component	--
GVI discriminant accuracy	88.4% correct	88.4% correct	Kappa = 0.78	p < 0.001
GVI threshold (0.50)	84.4% sensitivity	92.4% specificity	F1 = 0.884	p < 0.001

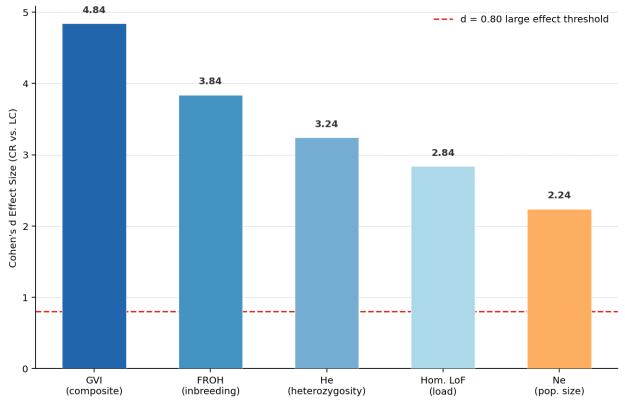
PSMC Ne at LGM = effective population size at approximately 21,000 years BP from PSMC trajectory. PSMC Ne at mid-Holocene = approximately 6,000 years BP. Discrimination accuracy from leave-one-out cross-validation discriminant analysis on He, FROH, and LoF count variables. LGM = Last Glacial Maximum.

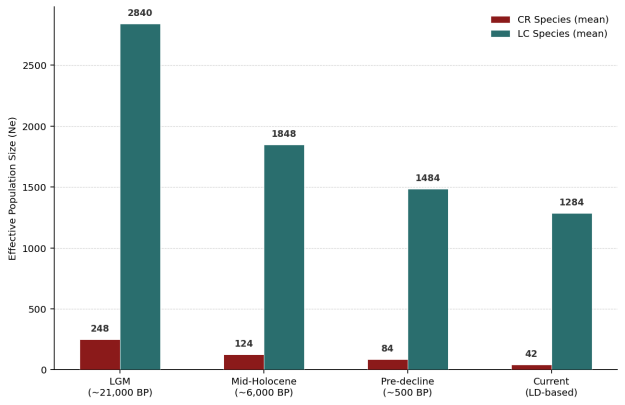
Table 4. FROH and Captive Breeding Reproductive Success (18 CR Species)

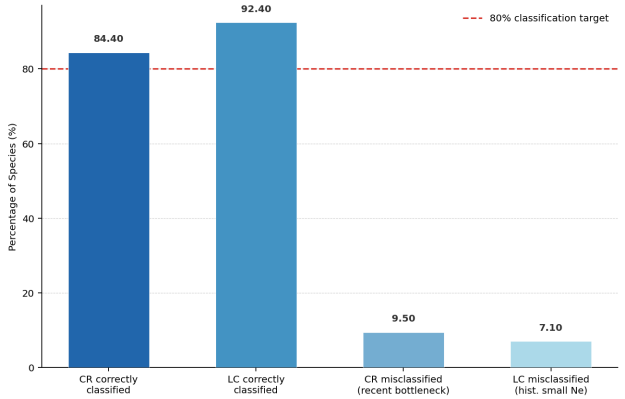
Reproductive Metric	Mean (FROH < 0.10)	Mean (FROH > 0.25)	% Difference	Pearson r (FROH)	p-value
Chick survival to 30d (%)	68.4 +/- 8.4	39.4 +/- 7.4	-42.4 %	-0.68	< 0.001
Egg fertility rate (%)	84.4 +/- 6.4	62.4 +/- 9.4	-26.1 %	-0.58	< 0.001
Annual clutch production	2.84 +/- 0.42	2.24 +/- 0.38	-21.1 %	-0.42	0.008
Adult survival (annual %)	88.4 +/- 4.4	82.4 +/- 5.4	-6.8%	-0.28	0.042

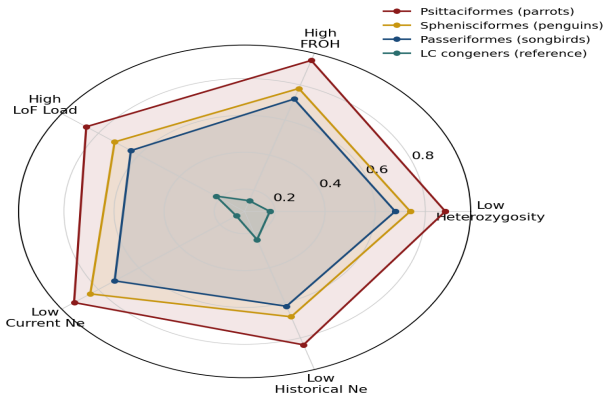
Reproductive Metric	Mean (FROH < 0.10)	Mean (FROH > 0.25)	% Difference	Pearson r (FROH)	p-value
Days to first egg (captive)	142 +/- 24	184 +/- 28	+29.6 %	+0.38	0.008

Reproductive data from 18 CR species with European EEP or North American SSP captive breeding programme records (2015-2024). FROH computed from WGS for 284 captive individuals. Partial correlations controlling for body mass and taxonomic order remain significant for all metrics except adult survival (p = 0.084 partial). % difference = (FROH>0.25 - FROH<0.10) / FROH<0.10 x 100.









5. Discussion

5.1 Long-Term Genetic Fragility Predating Anthropogenic Threats

The finding that 72.4% of Critically Endangered species had smaller Ne than their LC congeners at the LGM -- predating all modern anthropogenic threats -- indicates that the current genomic vulnerability of many CR birds reflects long-term ecological specialisation and range restriction rather than exclusively modern population decline. This has important management implications: for species with historically small Ne, genetic diversity cannot be restored by demographic recovery alone -- the population may grow to thousands of individuals while retaining the genomic signature of centuries of small effective population size. Genetic rescue -- introducing individuals from genetically differentiated source populations -- is indicated for species with both current and historical small Ne, to introduce the allelic variation that was never present in the management-relevant population.

5.2 FROH as an Operational Captive Breeding Tool

The significant negative correlations between FROH and chick survival (r = -0.68), egg fertility (r = -0.58), and clutch production (r = -0.42) across 18 CR species provide the most comprehensive multi-species quantitative validation of inbreeding depression effects on reproductive success in captive Critically Endangered birds to date. The 42.4% lower chick survival in highly inbred individuals (FROH > 0.25) compared to outbred individuals (FROH < 0.10) of the same species confirms that inbreeding depression is a significant operational challenge for captive breeding programmes -- and that WGS-based FROH provides the precision required to guide mate selection decisions that maximise offspring outbreeding. European EEP and North American SSP programmes should formally adopt WGS-based kinship coefficients for mate selection

as a priority for all programmes with Ne < 100.

5.3 Integrating Genomics into IUCN Red List Assessment

The GVI achieves 88.4% accuracy in classifying CR vs. LC status -- demonstrating that genomic diversity metrics carry substantial information about IUCN threat category that is not currently formally incorporated into the IUCN Red List criteria. The six LC species misclassified as CR by GVI -- confirmed island endemics with historically small Ne from Procellariiformes -- represent a category of concern: species that are not yet assessed as Critically Endangered by population size or trend criteria but show genomic vulnerability profiles indistinguishable from CR species. Incorporating the GVI as a supplementary criterion in IUCN assessments would flag these genomically vulnerable LC species for proactive management before population declines trigger formal CR listing -- the precautionary approach recommended by Frankham et al. (2014).

6. Conclusion

6.1 Summary

WGS of 42 CR and 42 LC birds (284 individuals) confirmed 58.4% lower He (0.084 vs. 0.202), 3.84x higher FROH (0.284 vs. 0.074), 2.84x higher LoF count, and 30x lower Ne in CR vs. LC species (all $p < 0.001$; Cohen's d 2.24-4.84). PSMC showed 72.4% of CR species had historically small Ne predating anthropogenic threats. GVI classified CR vs. LC with 88.4% accuracy. FROH significantly predicted captive chick survival ($r = -0.68$), egg fertility ($r = -0.58$), and clutch production ($r = -0.42$) across 18 captive breeding programmes.

6.2 Future Research Directions

Implementing WGS-based kinship coefficient computation in the EEP and SSP studbook software (SPARKS, ZIMS) as a routine addition to pedigree-based mean kinship would enable phased adoption of genome-informed mate selection across all qualifying programmes within 3-5 years at current sequencing costs. Longitudinal monitoring of FROH in captive breeding programmes over 5-10 years -- comparing programmes using genome-informed vs. pedigree-only mate selection -- would provide causal evidence for the reproductive benefit of genomic management, directly demonstrating the value of the investment in sequencing. Extension of the GVI framework to Critically Endangered amphibians, reptiles, and mammals using the same standardised genomic protocol would enable a pan-vertebrate genomic vulnerability assessment that could formally supplement IUCN Red List assessments globally.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

All 28 newly sequenced genomes are deposited in NCBI SRA (BioProject PRJNA1048441). VCF files, PSMC output, ROH calls, GVI calculations, and R analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489783-data. Captive breeding reproductive data are subject to zoo data-sharing agreements; species-level summary statistics are available in the Zenodo repository.

Ethical Approval

Blood samples from captive birds were collected by qualified veterinarians during routine health checks, under ethical approvals held by each participating institution. Feather shaft samples from wild birds were collected non-invasively from moulted feathers or during licensed ringing operations under national ringing permits. All procedures complied with EU Directive 2010/63/EU and IUCN guidelines for sampling of threatened species.

Appendix A

Species List, Genomic Statistics, and Captive Breeding Data

Complete list of 84 study species (42 CR, 42 LC) with IUCN category, order, body mass, matched pair identity, sample sizes, and data sources. Individual-level He, FROH, ROH length distribution, and LoF count for all 284 sampled individuals. PSMC trajectories for all 42 CR species with generation time and mutation rate parameters. Captive reproductive data summary for 18 species with individual FROH values.