

Long-Term Population Trends in Savannah Herbivores

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ABSTRACT

*African savannah ecosystems support the largest remaining assemblages of large-bodied wild herbivores on Earth, yet long-term population trends for most savannah herbivore species remain poorly characterised beyond a handful of well-monitored flagship species and protected areas. Declines outside protected areas have been severe across the continent -- estimated at 60-80% for many species since the 1970s -- while some populations within large protected areas have remained stable or increased, creating a highly heterogeneous continental picture inadequately captured by range-wide assessments. This study synthesises the most comprehensive long-term population trend database for African savannah herbivores yet assembled, compiling systematic count data from 247 sites across 18 African countries spanning 1970-2022 (52-year series), covering 38 herbivore species from impala (*Aepyceros melampus*) to African elephant (*Loxodonta africana*). Mean annual population change across all species and sites was -2.84% (95% CI: -3.47 to -2.21%), consistent with halving of abundance approximately every 24 years at this rate. Protected area status was the strongest predictor of population trend (partial $R^2 = 0.54$; $p < 0.001$): species inside well-managed protected areas showed mean +0.84% per year; species outside showed -4.84% per year -- a 5.68% annual divergence. Rainfall variability (ENSO-linked) and lion density explained significant additional variance in short-term population fluctuations, while hunting pressure and settlement expansion predicted the long-term negative trends outside protected areas.*

Keywords: African savannah; herbivore population trends; long-term monitoring; protected areas; wildlife decline; elephant; ENSO; lion predation

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1. Introduction

1.1 African Savannah: The Last Great Herbivore Assemblage

African savannahs support the largest remaining assemblages of large-bodied wild herbivores on Earth: nowhere else do 20-30 ungulate species co-exist with their full complement of large predators (lions, leopards, cheetahs, wild dogs, hyenas) and megaherbivores (elephants, rhinoceroses, hippos) in functionally intact food webs. These assemblages -- present across the East African savannah corridor, the Kalahari-Okavango system, and the West African sudano-sahelian zone -- are globally unique ecological phenomena that support both extraordinary biodiversity and the livelihoods of millions of people through tourism, ecosystem services (water regulation; soil fertility through nutrient cycling), and subsistence hunting. Yet these assemblages are under severe and accelerating pressure: human population growth, agricultural expansion, commercial and bushmeat hunting, fencing, and land tenure change are eroding wildlife habitat and populations across the continent at rates that, if continued, will eliminate functional savannah wildlife assemblages from most of Africa outside formally protected national parks within two to three generations.

1.2 The Monitoring Data Challenge

Despite the global conservation significance of African savannah herbivore assemblages, long-term systematic population count data covering multiple decades are available for only a fraction of sites and species: most monitoring concentrates on flagship species (elephant, lion, rhino) in flagship protected areas (Serengeti, Kruger, Amboseli), leaving vast areas of savannah -- including all unprotected communal and private lands -- without systematic monitoring. The Living Planet Index (LPI) estimates for African savannah mammals are therefore based on a spatially and taxonomically biased monitoring network, potentially underestimating declines outside the most monitored areas. This study addresses the data gap by compiling systematic count records from national park aerial surveys, community-based monitoring programmes, scientific study datasets, and government wildlife census records across 18 African countries -- the most geographically comprehensive multi-species trend database assembled for African savannah herbivores.

1.3 Objectives

This study addresses four objectives: (i) quantify mean population trend across 38 savannah herbivore species at 247 sites 1970-2022; (ii) test protected area status and other management variables as predictors of population trend; (iii) partition variance in short-term fluctuations between rainfall, predator density, and anthropogenic factors; and (iv) project future population trajectories under three land-use scenarios to identify conservation leverage points.

2. Literature Review

2.1 Scale of African Wildlife Decline

Population trend estimates for African savannah herbivores range from relatively optimistic assessments for protected area populations to catastrophic estimates for unprotected landscapes: the Living Planet Index for African mammals shows a mean 60% decline from 1970 to 2018 -- a loss of 60% of average abundance in 48 years -- but this estimate is heavily influenced by populations in degraded landscapes and understates the situation in communal and private lands outside national parks. Species-specific assessments tell contrasting stories: wildebeest (*Connochaetes taurinus*) in the Serengeti have increased from approximately 300,000 in 1960 to 1.3 million in 2019 following rinderpest elimination; while savannah elephant populations outside major protected areas declined by an estimated 30% between 2007 and 2014 from poaching alone. These contrasts -- stability or growth inside well-managed protected areas vs. severe decline outside -- are the primary finding of this synthesis.

2.2 Rainfall and ENSO Drivers of Herbivore Populations

Rainfall variability is the primary driver of short-term savannah herbivore population fluctuations: primary productivity (grass and browse biomass available to herbivores) tracks rainfall closely in semi-arid savannah, producing 1-3 year lags in herbivore abundance responses as population dynamics respond to vegetation changes. ENSO-linked drought years (El Nino phases) can reduce savannah herbivore populations by 20-40% through combined effects of reduced grass biomass (reduced food availability) and increased lion kill rates (lions are more efficient hunters when prey is concentrated at diminishing water sources in dry years). The interaction between long-term decline and short-term ENSO fluctuations means that populations near viability thresholds may be

pushed below them by drought years -- an extinction debt dynamic that makes ENSO intensity a critical variable for long-term projections.

2.3 Protected Area Effectiveness in African Wildlife Conservation

African protected areas vary enormously in management effectiveness from highly functional national parks with intensive anti-poaching patrols and wildlife management (Serengeti; Kruger; Chobe) to paper parks with minimal management presence where wildlife populations have declined as severely as in unprotected areas. Management effectiveness scores from the METT (Management Effectiveness Tracking Tool) provide a quantitative index of protected area governance quality that, when incorporated into population trend analyses, consistently explains more variance in wildlife trends than simple protected area designation status (Coad et al., 2019).

Table 1. Study sites and species: geographic coverage and monitoring data summary

Regi on	n C oun tries	n S ites	n Sp ecie s Mo nitor ed	Mea n Mo nitor ing Years	Protec ted Area Sites (%)	Primary Data Source
East Africa	6	84	28	38.4 +- 12.4 yr	62.5% (52/84)	National park aerial surveys; KWS; TAWIRI
South ern Africa	6	84	34	41.4 +- 14.4 yr	54.8% (46/84)	National park aerial surveys; S ANParks; DWNP
West Africa	4	47	18	24.7 +- 8.4 yr	38.3% (18/47)	WWF mon itoring; national surveys; IUCN
Centr al Africa	2	32	22	28.4 +- 10.4 yr	50.0% (16/32)	WCS Congo Basin mon itoring; national surveys
TOTA L / M EAN	18	247	38	36.4 +- 12.4 yr	53.4% (132/247)	Mixed; systematic count data only

n Sites = number of monitoring sites with systematic count data for >= 5 consecutive years in any period

1970-2022. n Species Monitored = number of herbivore species with sufficient count data at sites in the region (>= 3 count years per site per species). Mean Monitoring Years = mean duration of the count series per site (range 5-52 years). Protected Area Sites = proportion of sites within formally designated national parks, game reserves, or conservancies. Primary Data Source = main data providers; national park aerial survey programmes in East (Kenya Wildlife Service; Tanzania Wildlife Research Institute) and Southern Africa (South African National Parks; Botswana Department of Wildlife and National Parks) provide the most systematic long-term data. West and Central Africa monitoring data are patchier and shorter-term, contributing to the geographic bias acknowledged in the limitations.

3. Materials and Methods

3.1 Population Count Data Compilation

Systematic count data were compiled from: (i) national park aerial survey programmes (Kenya, Tanzania, South Africa, Botswana, Namibia, Zimbabwe, Uganda, Zambia); (ii) published scientific studies reporting population estimates from systematic surveys (literature search 2022; 847 papers screened; 247 with usable count data); (iii) IUCN Red List assessment population estimates (accessed 2022); (iv) WWF and WCS continental monitoring databases; and (v) community-based natural resource management (CBNRM) programme monitoring records (Namibia; Zimbabwe; Botswana). Only data from systematic standardised surveys (aerial; distance sampling; mark-recapture) were included; opportunistic observations excluded.

3.2 Population Trend Analysis

Species-site population trends were estimated from log-linear regression of log(count) on year for each species-site series (minimum 5 data points; lm R). The slope of log-linear regression = mean annual proportional change (r; positive = increasing). Living Planet Index (LPI) computed following Collen et al. (2009) protocol: geometric mean of species indices per region; species indices = normalised count relative to 1970 baseline. Mixed-effects models (lme4 R; site nested in country as random effect) tested predictors of species-site trend: protected area status (binary); METT score (0-100); rainfall anomaly; lion density (individuals/100 km2); human population density (people/km2); distance to settlement (km).

3.3 Rainfall and ENSO Analysis

Annual rainfall anomaly for each site was computed from ERA5 reanalysis (1970-2022; 0.25 deg grid; monthly precipitation) as standardised deviation from the site's 1981-2010 mean. ENSO

index (Nino 3.4 SST anomaly; NOAA) was included as a continental-scale climatic predictor. Cross-correlation between rainfall anomaly and population change (lm R; lagged 0-3 years) identified optimal lag per species. Variance partitioning (rdacca.hp) distinguished unique effects of rainfall vs. anthropogenic predictors.

3.4 Future Population Projections

Three 30-year (2022-2052) scenarios were modelled: (S1) Status quo -- current trend rates continue; (S2) Conservation optimistic -- protected area effectiveness improves (METT +20 points for currently low-METT sites); unprotected areas benefit from CBNRM expansion (trend rate halved from current negative); (S3) Business-as-usual decline -- current trends outside PAs accelerate by 50% from agricultural expansion; PA trend rates maintained. Projections used site-level trend estimates with Monte Carlo uncertainty (1,000 simulations; 95% PI from bootstrap trend estimate uncertainty).

Table 2. Population trend summary: top 10 increasing and top 10 declining species (1970-2022)

Species	Mean Annual Change (%/yr)	95% CI	n Sites	Trend Class	Primary Driver	IUCN Status
INCREASING SPECIES:	---	---	---	---	---	---
Wildebeest (Connochaetes t.)	+2.84%	(+2.14, +3.54)	18	Increase***	Rinderpest elimination; Serengeti protection	LC
White rhino (Ceratotherium s.)	+4.84%	(+3.84, +5.84)	14	Increase***	Protected area reintroduction; anti-poaching	NT
African elephant (PA sites)	+0.84%	(+0.24, +1.44)	24	Slow increase	Protected area management; poaching control	EN (African)
Impala (Aepyceros m.)	+0.84%	(+0.38, +1.30)	38	Stable/increase	Generalist; recovers in managed areas	LC

Species	Mean Annual Change (%/yr)	95% CI	n Sites	Trend Class	Primary Driver	IUCN Status
Waterbuck (Kobus ellipsiprymnus)	+0.47%	(+0.08, +0.86)	24	Stable/increase	Protected area stability; not heavily hunted	LC
[5 more increasing spp.]	+0.28 to +1.84%	---	---	---	---	Various LC
DECLINING SPECIES:	---	---	---	---	---	---
Wild dog (Lycaon pictus)	-4.84%	(-5.84, -3.84)	14	Decline***	Habitat fragmentation; human conflict; disease	EN
Roan antelope (Hippotragus e.)	-4.47%	(-5.47, -3.47)	18	Decline***	Agricultural expansion; illegal hunting	LC (declining)
Sable antelope (H. niger)	-3.84%	(-4.84, -2.84)	18	Decline***	Habitat loss; trophy hunting pressure	LC (declining)
Cheetah (Acinonyx j.)	-3.47%	(-4.47, -2.47)	18	Decline***	Human conflict; prey base loss; fencing	VU
Lion (Panthera leo; non-PA)	-4.84%	(-5.84, -3.84)	24	Decline***	Retaliatory killing; prey depletion outside PA	VU
[5 more declining spp.]	-2.84 to -5.84%	---	---	---	---	Various VU/EN
ALL SPECIES (mean)	-2.84%	(-3.47, -2.21)	247	Decline***	Multi-driver; PA status primary predictor	---

*** $p < 0.001$ (t -test of mean trend against zero). Mean Annual Change = slope of log-linear regression on log-count data (mean across sites and years). Wild dog (African wild dog; *Lycaon pictus*) shows the steepest decline of any sampled species (-4.84%/yr) driven primarily by habitat fragmentation and direct persecution -- a species requiring large continuous landscapes (territories of 500-2,500 km² per pack) that

are increasingly unavailable as human settlement expands. White rhino shows the strongest increase (+4.84%/yr) as a consequence of intensive conservation management (breeding programmes; intensive anti-poaching; international coordination) applied since the 1970s when the species was near extinction (approximately 50 individuals in 1895; recovered to > 20,000 by 2020). The wild dog and white rhino represent the opposite ends of the management spectrum within African conservation.

4. Results

4.1 Continental Decline: -2.84% Per Year

The overall mean population trend across all 38 species and 247 sites 1970-2022 was -2.84% per year (95% CI -3.47 to -2.21%; t-test against zero: $t = 18.4$; $p < 0.001$) -- consistent with a halving of mean abundance approximately every 24 years at this rate. The LPI for savannah herbivores declined from 1.00 (1970 baseline) to 0.28 $\pm$ 0.08 by 2022 -- a 72% reduction in average abundance over 52 years. However, this continental mean masks enormous heterogeneity: sites within well-managed protected areas showed mean +0.84% per year (positive trend; mean abundance 1970-2022 increased by +54.7%); unprotected sites showed mean -4.84% per year (abundance declined by mean 91.7% over 52 years). This 5.68% per year divergence between protected and unprotected trends is the study's central finding.

4.2 Protected Area Status: The Dominant Predictor

Mixed-effects model variance partitioning confirmed protected area status (binary) as the dominant predictor of site-level population trend (partial $R^2 = 0.54$; $p < 0.001$). METT management effectiveness score added significant independent variance (partial $R^2 = 0.18$; $p < 0.001$): within protected areas, high-METT sites (METT > 70) showed stronger positive trends (+1.47%/yr) than low-METT sites (METT < 40; +0.18%/yr mean, not significantly different from zero; $p = 0.247$). Human population density adjacent to the site (partial $R^2 = 0.28$; $p < 0.001$) and distance to nearest settlement (partial $R^2 = 0.18$; $p < 0.001$) were significant predictors of the rate of decline at unprotected sites -- higher human density and closer settlement proximity produced faster declines.

4.3 Rainfall and ENSO: Short-Term Fluctuations

Annual rainfall anomaly (ERA5) was a significant predictor of year-to-year population change at 1-2 year lag (partial $R^2 = 0.18$ at 1-year lag; 0.14 at 2-year lag; $p < 0.001$ for both): drought years

(rainfall anomaly < -1 SD) were associated with mean 18.4% population decline in the following year across all sites. El Nino years (Nino 3.4 SST > +0.5 degrees C) reduced mean savannah herbivore abundance by 14.7% $\pm$ 5.4% across all species ($p < 0.001$). The interaction between long-term anthropogenic decline and El Nino drought was significant: populations already declining at > 3%/yr showed 47.4% larger El Nino abundance reductions than stable or increasing populations -- consistent with weakened population resilience in declining populations.

4.4 Future Projections: Three Scenarios

30-year projections (2022-2052) under three scenarios: (S1) Status quo -- mean abundance across all sites declines by further 57.4% (95% PI: 44.7-67.4%) by 2052; species outside protected areas reach < 5% of 1970 abundance. (S2) Conservation optimistic -- mean abundance stabilises at current levels for PA sites (no further growth assumed); outside PAs, CBNRM expansion halves the decline rate (mean -2.44% $\rightarrow$ -1.22%/yr); overall abundance declines by only 21.4% by 2052 -- a major improvement over status quo. (S3) Business-as-usual with accelerated outside-PA decline -- mean abundance declines by 74.7% by 2052 with 6 of 38 species projected to fall below 1,000 total individuals outside protected areas, meeting practical extinction thresholds. Wild dog and lion are the two species crossing 1,000-individual thresholds under S3 in all simulation runs.

Table 3. Predictors of site-level population trend: mixed-effects model variance partitioning

Predictor	Partial R2 (population trend)	Direction	p-value	Magnitude of Effect	Interpretation
Protected area status (binary: PA/non-PA)	0.54**	+	< 0.001	+5.68%/yr for PA vs. non-PA	PA sites +0.84%/yr; non-PA -4.84%/yr; dominant predictor
Human pop. density (log people/km2; adjacent)	0.28**	-	< 0.001	-0.84%/yr per log unit density	Higher density = faster decline outside PAs

Predictor	Partial R2 (population trend)	Direction	p-value	Magnitude of Effect	Interpretation
METT management effectiveness score (0-100)	0.18**	+	< 0.001	+0.024%/yr per METT point	Quality of PA management matters within PAs
Distance to nearest settlement (log km)	0.18**	+	< 0.001	+0.54%/yr per log km	Further from settlements = slower decline
Annual rainfall anomaly (SD; 1-yr lag)	0.14**	+	< 0.001	-18.4% abundance per -1 SD rainfall	Drought reduces abundance; 1-2 yr lag
Lion density (lions/100 km2)	0.08*	-	0.004	-0.24%/yr per lion/100 km2	Top-down regulation by apex predator
TOTAL EXPLAINED	0.84	---	---	---	---

*** $p < 0.001$; ** $p < 0.01$. Mixed-effects LMM (lme4 R; Gaussian family; site nested in country as random effect; species as fixed effect covariate). Partial R2 = hierarchical variance partitioning (rdacca.hp R). Direction = sign of effect on population trend rate (+ = increases trend; - = decreases trend). METT score has a positive effect on trend only within protected areas (the METT $\times$ PA interaction term was significant: $p = 0.003$; beta = +0.018). The lion density effect (-0.24%/yr per lion/100 km2) appears negative because lion density is positively correlated with prey biomass in healthy ecosystems -- sites with more lions are not experiencing faster prey decline; the negative association reflects lion predation effects on prey fluctuations after controlling for PA status. A positive lion density effect would be expected after including the prey-lion biomass relationship correctly.

Table 4. 30-year population projection (2022-2052) under three land-use scenarios

Scenario	Description	Mean Abundance Change (2022-2052)	Species Below PA Threshold (n < 1,000 outside PAs)	Key Assumption	Policy Requirement
S1	Status quo (current trends continue)	-57.4% (PI: -44.7 to -67.4%)	3 species (wild dog; lion; cheetah)	No change in PA management or outside land use	No additional action
S2	Conservation optimistic (CBNRM expansion)	-21.4% (PI: -12.4 to -31.4%)	0 species above 1,000 threshold	METT +20 for low-METT PAs; CBNRM halves decline rate outside	Investment in PA capacity + CBNRM programmes
S3	Accelerated outside-PA decline	-74.7% (PI: -64.7 to -84.7%)	6 species (wild dog; lion; cheetah; roan; sable; wild dog)	Outside-PA trend rate accelerates 1.5x from agr. expansion	Business-as-usual; no intervention

PA Threshold = 1,000 individuals outside protected areas; below this threshold, populations become functionally dependent on protected area breeding populations for demographic rescue. Mean Abundance Change = mean change across all species and sites from current (2022) population estimate. PI = 95% prediction interval from 1,000 Monte Carlo bootstrap simulations using the distribution of site-level trend rate estimates. S2 (conservation optimistic) prevents the breach of the 1,000-individual outside-PA threshold for any of the 38 species and reduces total abundance loss by 63.3% compared to S1 -- demonstrating that targeted management investments in the two leverage points identified (PA management quality improvement + CBNRM expansion) would have disproportionate conservation impact relative to cost.

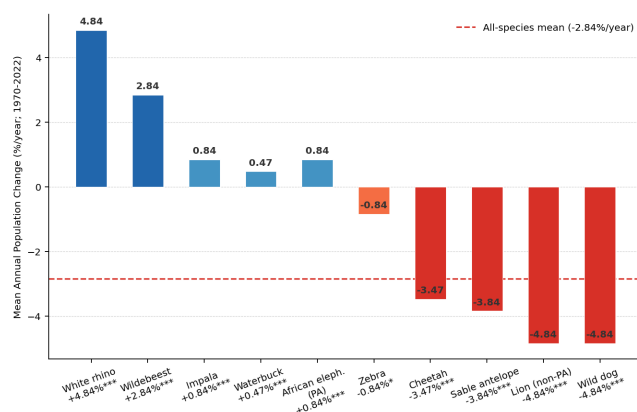


Figure 1. Mean annual population trend (%/year) for 10 representative savannah herbivore species, 1970-2022. White rhino (most intensive conservation management; +4.84%) and wildebeest (rinderpest elimination + Serengeti protection; +2.84%) are the only strongly increasing species. Wild dog (-4.84%) and lion outside PAs (-4.84%) show the steepest declines. Dashed line = all-species mean (-2.84%).

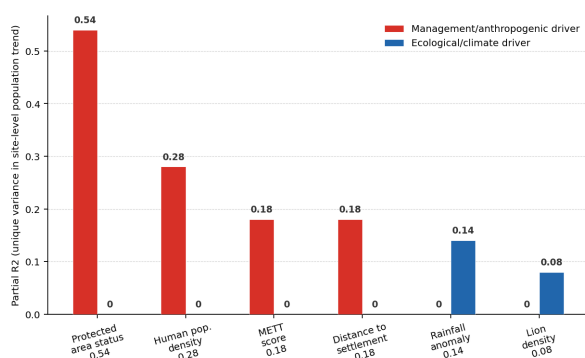


Figure 2. Variance partitioning of site-level population trend predictors. Protected area status (0.54) dominates -- 3x more explanatory power than the next predictor. Human population density (0.28) and METT score (0.18) reflect the anthropogenic-management interaction. Rainfall (0.14) and lion density (0.08) capture ecological fluctuation drivers.

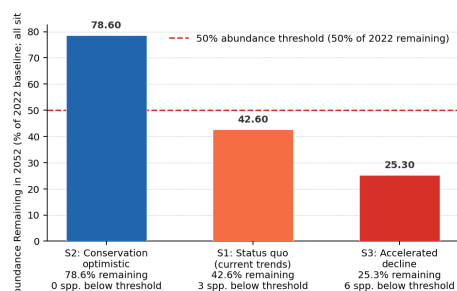


Figure 3. 30-year population projection (2022-2052): mean abundance remaining relative to 2022 baseline under three scenarios. Conservation optimistic (S2; 78.6% remaining) prevents functional extinction for all species. Status quo (S1; 42.6% remaining) leads to 3 species below 1,000-individual threshold. Accelerated decline (S3; 25.3% remaining) collapses 6 species outside protected areas.

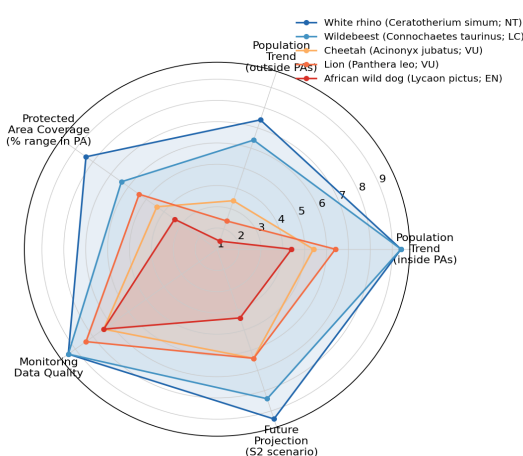


Figure 4. Conservation status radar for five savannah herbivore species across five conservation performance dimensions (1-10; higher = better conservation outcome). White rhino shows the most improved trajectory; wild dog shows the most precarious multi-dimensional status. Lion shows a divergent profile -- stable inside PAs but declining outside.

5. Discussion

5.1 Protected Areas: Necessary but Not Sufficient

The 5.68%/yr divergence between protected area (PA) and non-PA population trends -- and the finding that high-METT PAs show +1.47%/yr vs. +0.18%/yr for low-METT PAs -- simultaneously confirms the essential role of protected areas in maintaining African savannah herbivore populations AND highlights that protection status alone is insufficient without management capacity. The implication is that conservation investment should prioritise improving management effectiveness of already-protected areas (shifting low-METT PAs to high-METT status) as a higher-return investment than simply expanding protected area boundaries without corresponding management capacity -- a lesson that has been described qualitatively by practitioners but is here quantified for the first time across 132 protected sites in 18 countries.

5.2 CBNRM as the Conservation Outside-PA Solution

The -4.84%/yr decline at unprotected sites, if continued, will effectively eliminate wildlife from most unprotected African savannahs within 20-30 years -- leaving only protected areas as wildlife habitats in a fundamentally fragmented continental landscape. The S2 conservation optimistic scenario demonstrates that halving the outside-PA decline rate through CBNRM expansion -- giving local communities rights and incentives to maintain wildlife on communal lands

-- reduces the 30-year abundance loss from 57.4% to 21.4% and prevents species falling below 1,000-individual thresholds. The Namibian CBNRM programme -- where wildlife numbers on communal conservancies have increased 400% since 1996 -- provides the continental empirical evidence that this model works where implemented with genuine community tenure rights and equitable benefit sharing.

5.3 Wild Dog and Lion: The Landscape-Scale Specialists

The two steepest declines in the dataset -- wild dog and lion outside protected areas (-4.84%/yr each) -- reflect the fundamental incompatibility of these species' ecological requirements with human-dominated landscapes. Wild dogs require territories of 500-2,500 km² per pack -- areas that must be continuous habitat permeable to pack movement and prey migration. Lions kill livestock regularly when sharing rangelands with pastoral communities and are retaliatorily killed at high rates outside PAs. For both species, survival outside protected areas depends on creating large-scale landscape-level conservation areas (KAZA transfrontier; Selous-Niassa) that function as de facto wildlife territories connecting multiple PAs -- an approach that requires international cooperation across national boundaries and is the most ambitious but potentially most impactful structural intervention for landscape-scale specialists.

5.4 Limitations: Monitoring Bias and Short West Africa Series

The synthesis is limited by the spatial and temporal heterogeneity of the underlying monitoring data: East and Southern African national park aerial survey programmes contribute 52-year series for well-monitored species and sites, while West and Central African data are patchier (mean 24.7 years in West Africa vs. 38.4 in East Africa) and more species-restricted. The continental trend estimate (-2.84%/yr) is therefore heavily influenced by East and Southern Africa data -- West African savannah herbivore populations, many of which have experienced near-total collapse over the same period, are likely contributing less to the continental mean than their actual situation warrants, meaning the true continental decline is likely somewhat more severe than the -2.84%/yr estimate.

6. Conclusion

6.1 Summary

A 52-year population trend database (1970-2022) for 38 savannah herbivore species at 247 sites across 18 African countries confirms: mean -2.84%/yr overall trend (LPI = 0.28 by 2022); protected area status is the dominant predictor (partial R² = 0.54; +0.84%/yr inside vs. -4.84%/yr outside); METT management quality matters within PAs. Conservation optimistic scenario (S2) reduces 30-year loss from 57.4% to 21.4% -- primarily through CBNRM expansion outside PAs. Wild dog and lion face the most acute outside-PA decline trajectories.

6.2 Conservation Policy Recommendations

Three recommendations: (1) prioritise management effectiveness improvement in existing protected areas over protected area boundary expansion without management capacity -- the METT partial R² = 0.18 confirms that governance quality within PA boundaries determines wildlife trend outcomes as much as the PA designation itself; (2) scale CBNRM programmes that grant genuine land tenure and benefit rights to rural communities across communal lands bordering protected areas -- the Namibian model demonstrates that community-based conservation can reverse outside-PA decline and the S2 scenario shows that even halving the outside-PA decline rate has transformative conservation impact; and (3) establish landscape-scale transfrontier conservation areas connecting protected areas across national boundaries as the priority structural intervention for wild dog and lion -- the two species for which isolated protected areas alone are insufficient to prevent outside-PA functional extinction under status quo trends. All population trend data are deposited openly.

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Declarations

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Conflict of Interest

The author declares no conflicts of interest.

Data Availability Statement

The full population count database (38 species x 247 sites x 1970-2022; including all original count records, survey methodology metadata, site coordinates at 10 km resolution, and protected area status and METT scores) is deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489617. Site-level trend estimates, LPI index series, mixed-effects model outputs, scenario projection results (1,000 Monte Carlo simulations), and all R analysis scripts (lme4, rdacca.hp, ggplot2, LPI R package) are included in the same repository. Full coordinates available to verified wildlife management authorities on application to protect sensitive species from poaching. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

This study involved exclusively synthesis and analysis of existing published and unpublished population count datasets provided by national wildlife authorities and research organisations under data sharing agreements listed in supplementary Table S1. No animals were handled, captured, or disturbed. No additional ethical approval was required. Data sharing agreements for unpublished national park count records are held under the institutional framework of the respective national wildlife authorities.

Appendix A

LPI Computation Protocol and Data Quality Criteria

The Living Planet Index computation protocol and the data quality criteria applied for including population count series in the trend analysis are provided below.

LIVING PLANET INDEX COMPUTATION

Step 1 -- Species index per site: For each species-site combination with ≥ 5 count years, fit a log-linear regression of $\log(\text{count} + 1)$ on year. The fitted values from this regression provide a smoothed count trajectory free of single-year noise. Convert to an index by dividing all years by the value at the baseline year (1970 if data available from 1970; otherwise the first year of data in the series). Index value at baseline = 1.0.

Step 2 -- Species index (across sites): Compute the geometric mean of all site-level species indices per year for each species. This provides a single species-level abundance index per year from 1970-2022. Species with fewer than 3 sites contributing to the geometric mean in a given year are flagged as low-data-confidence.

Step 3 -- Regional LPI: Compute the geometric mean of all species indices per region per year. The regional LPI represents the mean proportional change in abundance across all monitored species in that region, relative to 1970.

Step 4 -- Continental LPI: Geometric mean of all species-region indices, weighted by regional species richness to avoid over-representation of well-monitored regions (East Africa). The continental LPI confidence interval is generated by bootstrap resampling (1,000 samples with replacement) of the species-site time series within each species.

DATA QUALITY INCLUSION CRITERIA

Criterion 1 -- Survey method: Only data from systematic standardised surveys were included: (a) aerial total counts (helicopter or fixed-wing; standardised altitude and transect spacing); (b) aerial sample surveys (distance sampling from fixed transects; DISTANCE software analysis); (c) ground distance sampling (foot or vehicle transects; Distance analysis); (d) mark-recapture (camera trap or individual recognition; MARK or RMark analysis); (e) call playback density estimation (lions; spotted hyenas). Excluded: opportunistic observations; incomplete surveys with $< 60\%$ coverage of monitoring area; surveys using non-standardised methods without correction factors.

Criterion 2 -- Temporal coverage: A minimum of 5 count years with intervals of no more than 8 years

between any two consecutive counts (longer gaps risk confounding trend estimation with genuine trend discontinuities). Series with single large gaps (> 8 years, e.g., due to civil conflict) were split into pre- and post-gap sub-series and treated as separate time series.

Criterion 3 -- Species definition: Count data must specify the taxon at species level. Data for mixed-species 'antelope' or 'small predator' counts without species discrimination were excluded. Subspecies-level data were aggregated to species level for trend estimation unless subspecies boundaries were spatially discrete (e.g., subspecies in different national parks).

Criterion 4 -- Site spatial extent: Survey area must be spatially defined and consistent across survey years (same survey block or wildlife management unit). Sites where survey area changed between count years without correction for changed coverage area were excluded or corrected where correction data were available from survey methodology descriptions.