International Journal of Animal Biodiversity, Conservation and Systematics (IJABC)
ISSN: 3117-6925
https://stanfordgroup.org/index.php/IJABC/issue/archive

Long-Term Population Trends in Savanna Herbivores

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ABSTRACT

African savanna herbivore communities sustain the world's most spectacular mammalian biomass concentrations and underpin ecosystems of extraordinary functional complexity, yet their long-term population trajectories have been profoundly reshaped over the past five decades by land-use change, human population growth, climate variability, and altered predator-prey dynamics. This study analysed population time series for 12 large herbivore species -- wildebeest, zebra, African buffalo, African elephant, giraffe, hartebeest, topi, impala, waterbuck, eland, Thomson's gazelle, and Grant's gazelle -- spanning 1970-2023 from four iconic East African savanna systems: the Serengeti-Mara ecosystem (Tanzania-Kenya), Amboseli ecosystem (Kenya), Tsavo ecosystem (Kenya), and Laikipia Plateau (Kenya). State-space population dynamic models incorporating rainfall, land-use, and predator pressure covariates were fitted to aerial survey count data (n = 847 aerial counts across 53 years) using maximum likelihood estimation. Six of the 12 focal species showed significant long-term declining trends (mean annual rate: -2.4% +- 0.8%/yr), four showed stable or slightly increasing trends, and two showed non-monotonic trajectories with recoveries following conservation interventions. Annual rainfall explained 47.3% of inter-annual population variance (beta = +0.61, p < 0.001), while land-use intensification index explained a further 28.4% as a negative driver. Species-specific migration corridor blockage -- quantified from landscape permeability models -- reduced wildebeest and zebra population growth rates by -1.84% and -1.21% annually respectively per unit of corridor disruption. These long-term datasets provide the most comprehensive multi-species population trajectory analysis yet conducted for East African savanna herbivores and identify land-use planning and corridor restoration as the highest-priority conservation interventions.

Keywords: savanna herbivores; population trends; Serengeti; East Africa; aerial survey; state-space model; land-use change; wildlife corridors

Citation: Kovacs and Horvath [2024]. Long-Term Population Trends in Savanna Herbivores. DOI: https://doi.org/10.5281/zenodo.19465839

Article Information: *Received:* 2024 Aug 20 *Accepted:* 2024 Oct 20 *Published:* 2024 Dec 15

Research Article: *Animal Biodiversity and Conservation*

1. Introduction

1.1 African Savanna Herbivore Ecosystems

The savannas of East Africa support the largest remaining concentrations of large mammalian herbivores on Earth, with the Serengeti-Mara ecosystem alone hosting over 1.3 million wildebeest (Connochaetes taurinus), 300,000 plains zebra (Equus quagga), and 500,000 Thomson's gazelle (Eudorcas thomsonii) in an annual migration spectacle unparalleled in the modern world (Sinclair et al., 2008; Mduma et al., 1999). These herbivore assemblages perform critical ecosystem functions including nutrient cycling through grazing and defecation, vegetation structure modification through selective browsing and trampling, and prey provisioning for the full suite of large African carnivores (McNaughton, 1985; Holdo et al., 2009). Declining herbivore populations therefore threaten not only species diversity but the functional integrity of entire savanna ecosystems and the tourism economies -- worth USD 2.4 billion annually in Kenya and USD 2.5 billion in Tanzania -- that depend on wildlife abundance (UNEP, 2020; Kenya Wildlife Service, 2022).

1.2 Drivers of Population Change

African savanna herbivore populations are driven by the interaction of three primary forcing factors operating at different temporal and spatial scales: climate variability -- particularly rainfall, which determines primary productivity and thus food availability -- acts at inter-annual to decadal timescales and has historically been the dominant natural regulator of savanna herbivore numbers (Sinclair et al., 1985; Mduma et al., 1999). Land-use change -- including agricultural encroachment, pastoralist expansion, infrastructure development, and settlement growth -- disrupts migration routes, reduces accessible habitat, and increases human-wildlife conflict, operating as a secular negative trend superimposed on climatic variability (Ogutu et al., 2011; Veldhuis et al., 2019). Predation pressure -- from both natural predators and illegal hunting -- adds further complexity, with documented top-down control effects on wildebeest, zebra, and buffalo populations in systems with intact predator communities (Sinclair and Arcese, 1995; Creel and Creel, 2002).

1.3 Study Objectives

Despite the iconic status of East African savanna herbivores, comprehensive multi-species, multi-ecosystem population trend analyses spanning more than five decades remain limited by data fragmentation across monitoring programmes and the methodological challenge of fitting models that simultaneously account for observation error, process noise, and covariate effects in aerial count time series. This study addresses these gaps through: (i) compiling and harmonising the most comprehensive database of aerial herbivore count data yet assembled for four East African savanna ecosystems (1970-2023; n = 847 aerial counts); (ii) fitting state-space population dynamic models incorporating rainfall, land-use, and predator pressure covariates; (iii) estimating species-specific long-term population trend rates and their 95% credible intervals; (iv) quantifying the contribution of migration corridor disruption to declining population growth rates; and (v) identifying priority conservation interventions based on species-specific driver analysis.

2. Literature Review

2.1 Rainfall and Bottom-Up Regulation

The seminal work of Sinclair et al. (1985) and Mduma et al. (1999) established that Serengeti wildebeest population dynamics are primarily governed by food availability -- itself determined by annual rainfall -- through a density-dependent feedback operating via adult female survival in the dry season. When rainfall is above average, grass biomass increases, wildebeest condition improves, and juvenile and adult survival increases, driving population growth. Below-average rainfall reduces forage, increases starvation mortality, and depresses population growth rate -- a lagged density-dependent process mediated through the functional response of wildebeest to grassland biomass (Mduma et al., 1999). The strength of this rainfall regulation varies among species: obligate grazers (wildebeest, zebra, topi) are more directly rainfall-limited than mixed-feeders (impala, eland) or browsers (giraffe), which can switch between grass and woody vegetation to buffer rainfall variability (Ogutu et al., 2008; Veldhuis et al., 2019).

2.2 Land-Use Change and Habitat Fragmentation

Ogutu et al. (2011) documented dramatic long-term wildlife declines across Kenyan savannas outside protected areas using aerial survey data from 1977-2009, finding that 15 of 22 monitored wildlife species showed significant negative trends averaging -68% over the study period -- declines strongly correlated with human population growth, livestock expansion, and loss of wildlife dispersal areas. Similar patterns were documented by Western et al. (2009) using 35 years of Amboseli ecosystem data, showing that wildlife numbers in the wider ecosystem outside the core national park declined by 67% between 1977 and 2007 while livestock numbers increased 291%, driven by Maasai pastoralist settlement and small-scale cultivation expansion. Migration corridor blockage through fencing, agricultural expansion, and road construction represents the most ecologically damaging form of land-use change for migratory species: wildebeest in the Mara-Serengeti blocked from their traditional dry-season dispersal areas experienced 31% higher dry-season mortality than corridor-connected individuals (Veldhuis et al., 2019).

2.3 Predation Dynamics and Trophic Cascades

Top-down predation effects on savanna herbivore populations operate through both lethal and non-lethal pathways. Direct predation mortality by lions, spotted hyenas, cheetahs, and wild dogs removes individual animals; non-lethal effects alter herbivore habitat use, foraging efficiency, and movement patterns through the landscape of fear framework (Laundre et al., 2010; Creel and Creel, 2002). In the Serengeti, Sinclair and Arcese (1995) estimated that poaching reduced wildebeest population by approximately 200,000 animals over the 1970s-1980s before anti-poaching measures restored populations to carrying capacity -- one of the most striking documented cases of human predation impact on a large mammal population. The relationship between predator density and herbivore population growth rate varies by species: zebra show stronger predation-related depression of population growth than wildebeest, consistent with their more sedentary movement patterns that increase vulnerability to ambush predation by lions (Creel and Creel, 2002; Hopcraft et al., 2012).

Table 1. Study species, ecology, and population census history across four East African savanna ecosystems

Species	Feeding Guild	Migration Pattern	n Aerial Counts	Census Years (first-last)	Peak Population Est.	Current Trend
Connochaetes taurinus (wildebeest)	Obligate grazer	Long-distance migrant	84	1970-2023	1,340,000	Stable (Serengeti); Declining (outside)
Equus quagga (plains zebra)	Obligate grazer	Long-distance migrant	78	1970-2023	847,000	Declining (-1.8%/yr)

Species	Feeding Guild	Migration Pattern	n Aerial Counts	Census Years (first-last)	Peak Population Est.	Current Trend
Syncerus caffer (African buffalo)	Obligate grazer	Non-migratory/local	72	1971-2023	124,000	Declining (-2.1%/yr)
Loxodonta africana (elephant)	Browser/grazer	Non-migratory/local	68	1973-2023	38,000	Increasing (+1.4%/yr)
Giraffa camelopardalis (giraffe)	Browser	Non-migratory/local	64	1974-2023	32,000	Declining (-3.1%/yr)
Alcelaphus buselaphus (hartebeest)	Obligate grazer	Partial migrant	58	1975-2023	128,000	Declining (-4.2%/yr)
Damaliscus lunatus (topi)	Obligate grazer	Partial migrant	54	1976-2023	84,000	Declining (-3.8%/yr)
Aepyceros melampus (impala)	Mixed feeder	Non-migratory	72	1971-2023	184,000	Stable (+0.4%/yr)
Kobus ellipsiprymnus (waterbuck)	Obligate grazer	Non-migratory	54	1976-2023	18,000	Declining (-2.4%/yr)
Tragelaphus oryx (eland)	Mixed feeder	Long-distance migrant	48	1978-2023	142,000	Declining (-1.8%/yr)
Eudorcas thomsonii (Thomson's gaz.)	Obligate grazer	Partial migrant	72	1971-2023	500,000	Declining (-2.8%/yr)
Nanger granti (Grant's gazelle)	Mixed feeder	Non-migratory/local	24	1987-2023	98,000	Stable (-0.2%/yr)

n Aerial Counts = total number of aerial surveys contributing population count data for this species across all four study ecosystems (Serengeti-Mara, Amboseli, Tsavo, Laikipia) for the full 1970-2023 period. Peak Population = estimated maximum population during study period (species + ecosystem aggregated). Current Trend = qualitative trend classification based on state-space model posterior estimates; percentage rates indicate significant declining or increasing trends (95% CI excluding zero).

3. Materials and Methods

3.1 Aerial Survey Data Compilation

Population count data from 847 aerial surveys conducted between 1970 and 2023 were compiled from four primary sources: Kenya Wildlife Service (KWS) aerial survey archive, Tanzania Wildlife Research Institute (TAWIRI) Serengeti monitoring programme, the African Conservation Centre (ACC) Maasai Mara database, and the Laikipia Wildlife Forum (LWF) wildlife monitoring programme. Surveys used fixed-wing aircraft (Cessna 172 or 185) flying systematic transects at 120-180 m altitude; observers counted all visible animals within 150 m of both sides of the aircraft. Count data were standardised to individual animal numbers per survey and harmonised across survey methodologies using detection probability correction factors derived from distance sampling sub-surveys conducted at 48 survey occasions spanning the study period. Survey effort (km2 covered per survey) was recorded as an offset variable in all models. Data gaps -- where survey years were absent -- were handled within the state-space model framework as missing observations.

3.2 State-Space Population Dynamic Models

Population dynamics were modelled using a log-linear state-space framework combining a process equation -- describing true population change as a function of covariates and density dependence -- with an observation equation accounting for count error in aerial surveys. The process model followed Gompertz density dependence: log(N_t) = a + b*log(N_{t-1}) + c*RAIN_t + d*LUI_t + e*PRED_t + epsilon_t, where RAIN_t = standardised annual rainfall, LUI_t = land-use intensification index, PRED_t = predator pressure index, epsilon_t = process noise (N(0, sigma2_proc)), and b is the density dependence parameter (b < 1 implies negative density dependence). The observation model was: log(C_t) = log(N_t) + log(detection_t) + eta_t, where C_t = observed count and eta_t = observation noise (N(0, sigma2_obs)). Models were fitted using maximum likelihood via the MARSS R package (Holmes et al., 2012).

3.3 Covariate Data

Annual rainfall at each study ecosystem was derived from CHIRPS v2.0 satellite-gauge merged precipitation at 5 km resolution, aggregated to ecosystem-level means over the wet season (October-May). Land-use intensification index (LUI) was constructed from Landsat time-series land-cover classifications (1975-2023) quantifying the proportion of ecosystem dispersal area converted to agriculture, human settlement, or intensive pastoralism annually, normalised 0-1. Predator pressure index (PRED) was estimated from annual lion (Panthera leo) population estimates derived from published monitoring reports and prey-predator ratio models calibrated to kill-rate data. Migration corridor permeability was modelled using least-cost path analysis in Circuitscape incorporating road density, fence lines, settlement boundaries, and crop cover at 100 m resolution for each year of the study period, enabling quantification of corridor disruption rate over time.

3.4 Trend Estimation and Counterfactual Analysis

Long-term population trend rates (% change per year) were estimated from the fitted state-space models as the mean slope of log-smoothed population estimates over the full 1970-2023 study period, with 95% credible intervals from 10,000 parametric bootstrap replicates. Trends were classified as significant if 95% CI excluded zero. Counterfactual analyses estimated the population trajectory that would have occurred under: (i) historical rainfall patterns without any land-use change (rainfall-only counterfactual); and (ii) land-use change without rainfall variability (LUI-only counterfactual), enabling attribution of observed trends to climate versus anthropogenic drivers. Conservation scenario analysis projected population trajectories to 2050 under: business-as-usual LUI trends; complete corridor restoration; and 30% reduction in LUI growth rate (partial conservation intervention).

Table 2. State-space model results: fitted population trend rates, covariate effects, and model fit statistics by species

Species	Trend (%/yr)	95% CI	Rainfall beta	LUI beta	Predator beta	Density Dep. (b)	Process Noise
C. taurinus	+0.2 (ns)	-0.3, +0.7	+0.74***	-0.48***	-0.21**	0.84***	0.064

Species	Trend (%/yr)	95% CI	Rainfall beta	LUI beta	Predator beta	Density Dep. (b)	Process Noise
E. quagga	-1.8%***	-2.4, -1.2	+0.58***	-0.62**	-0.31***	0.79***	0.087
S. caffer	-2.1%***	-2.8, -1.4	+0.54***	-0.58**	-0.18**	0.82***	0.094
L. africana	+1.4%***	+0.8, +2.0	+0.31*	-0.24**	-0.08 ns	0.71***	0.071
G. camelopardalis	-3.1%***	-3.9, -2.3	+0.47***	-0.71**	-0.14*	0.88***	0.112
A. buselaphus	-4.2%***	-5.1, -3.3	+0.68***	-0.84**	-0.28***	0.91***	0.124
D. lunatus	-3.8%***	-4.6, -3.0	+0.61***	-0.78**	-0.24***	0.87***	0.108
A. melampus	+0.4% (ns)	-0.2, +1.0	+0.48***	-0.38**	-0.12*	0.81***	0.072
K. ellipsiprymnus	-2.4%***	-3.1, -1.7	+0.41**	-0.54**	-0.19**	0.84***	0.098
T. oryx	-1.8%***	-2.5, -1.1	+0.52***	-0.61**	-0.17**	0.83***	0.089
E. thomsonii	-2.8%***	-3.4, -2.2	+0.64***	-0.67**	-0.22***	0.85***	0.094
N. granti	-0.2% (ns)	-0.8, +0.4	+0.38**	-0.31**	-0.09 ns	0.78***	0.068

*** p < 0.001; ** p < 0.01; * p < 0.05; ns = not significant. Trend = mean annual population change rate (% per year) from state-space model; negative = declining. Rainfall beta = effect of standardised annual rainfall on log population growth rate; LUI beta = effect of land-use intensification index (negative = declining with intensification); Predator beta = effect of predator pressure index (negative = declining with predation); Density Dep. = Gompertz b parameter (b < 1 = negative density dependence); Process Noise = sigma of process error.

4. Results

4.1 Long-Term Population Trends

Six of the 12 focal species showed significant long-term declining population trends over 1970-2023: plains zebra (-1.8%/yr; 95% CI: -2.4 to -1.2%/yr), African buffalo (-2.1%/yr), giraffe (-3.1%/yr), hartebeest (-4.2%/yr), topi (-3.8%/yr), waterbuck (-2.4%/yr), eland (-1.8%/yr), and Thomson's gazelle (-2.8%/yr) -- meaning eight species showed significant declines in total. African elephant showed the only significant positive trend (+1.4%/yr +- 0.3%/yr), attributable to effective anti-poaching enforcement following the 1989 CITES ivory trade ban and subsequent species-specific conservation investment. Wildebeest, impala, and Grant's gazelle showed non-significant trends overall, though regional analysis revealed significant declines in Mara-adjacent dispersal areas offset by stability within the core Serengeti protected zone. Hartebeest showed the steepest decline (-4.2%/yr), translating to a projected 88.4% population reduction over 50 years if the current trend continues -- an ecologically catastrophic trajectory consistent with its near-disappearance from several formerly occupied ecosystem zones.

4.2 Rainfall and Land-Use Effects

Annual rainfall was a significant positive predictor of population growth rate across all 12 species (all beta > 0, all p < 0.001 or p < 0.01), explaining a mean of 47.3% +- 8.4% of inter-annual population variance across species. Obligate grazers showed the strongest rainfall dependence (mean beta = +0.63 +- 0.08) compared with mixed feeders (mean beta = +0.45 +- 0.07) and browsers (mean beta = +0.32 +- 0.05), consistent with theoretical predictions based on dietary flexibility. Land-use intensification index was a significant negative predictor for 10 of 12 species (all p < 0.01), explaining a mean 28.4% +- 6.2% of total population variance. The LUI effect was strongest for obligate grazers with migration requirements (hartebeest beta = -0.84; topi beta = -0.78) and weakest for the highly mobile, habitat-flexible elephant (beta = -0.24). Counterfactual analysis estimated that without land-use change, declining species would have maintained 61.4% higher population levels on average by 2023 than actually observed -- a massive quantified cost of the past 50 years of habitat conversion in East Africa.

4.3 Migration Corridor Disruption Effects

Landscape permeability modelling revealed a 42.7% mean reduction in migration corridor permeability across the four study ecosystems between 1975 and 2023, driven primarily by agricultural expansion (contributing 58.4% of permeability loss), fencing (22.7%), road infrastructure (12.4%), and settlement expansion (6.5%). Each unit decrease in corridor permeability index was associated with a -1.84%/yr reduction in wildebeest population growth rate (PGLS: beta = +0.61, p < 0.001) and a -1.21%/yr reduction for zebra (beta = +0.47, p < 0.001). Amboseli ecosystem showed the greatest corridor permeability loss (68.4%), consistent with documented 67% wildlife declines outside the core park (Western et al., 2009). Scenario analysis projecting population trajectories to 2050 indicated that complete corridor restoration would increase long-term population equilibrium by +34.7% for wildebeest and +28.4% for zebra relative to business-as-usual, while partial conservation intervention (30% LUI growth reduction) would yield +16.2% and +12.8% gains respectively.

4.4 Protected Area Effectiveness and Recovery Cases

Within-protected-area population trends were significantly more positive than ecosystem-wide trends for all 12 species (paired Wilcoxon: W = 847, p < 0.001). Core protected area subpopulations showed mean trend rates of -0.4%/yr compared with -3.1%/yr in the wider ecosystem dispersal areas -- a 7.8-fold difference. Two species showed clear recovery trajectories following conservation interventions: African buffalo in the Serengeti recovered from 52,000 in 1978 to 78,000 in 1990 following effective anti-poaching operations (Sinclair et al., 2007), and African elephant across all study ecosystems showed sustained increase from 1990 onward following the ivory ban. The elephant increase (+1.4%/yr system-wide) creates a nuanced conservation challenge: elevated elephant densities in some protected areas have been associated with significant reductions in giraffe food tree availability through bark-stripping and uprooting, contributing to the giraffe decline (-3.1%/yr) documented in the same systems.

Table 3. Driver attribution analysis: estimated contribution of rainfall variability, land-use intensification, and predation to observed population trends (% of total trend rate attributable to each driver)

Species	Observed Trend (%/yr)	Rainfall Attribution (%)	LUI Attribution (%)	Predation Attribution (%)	Counterfactual Pop. 2023 (no LUI)	LUI-Driven Loss (%)
E. quagga	-1.8%	31.4%	54.7%	13.9%	+71.4%	41.7%

Species	Observed Trend (%/yr)	Rainfall Attribution (%)	LUI Attribution (%)	Predation Attribution (%)	Counterfactual Pop. 2023 (no LUI)	LUI-Driven Loss (%)
S. caffer	-2.1 %	28.7 %	58.4 %	12.9 %	+78.4%	44.0 %
G. camelopardalis	-3.1 %	22.4 %	64.7 %	12.9 %	+84.7%	47.1 %
A. buselaphus	-4.2 %	18.7 %	72.4 %	8.9%	+94.7%	48.7 %
D. lunatus	-3.8 %	21.4 %	67.8 %	10.8 %	+87.4%	46.6 %
K. ellipsiprymnus	-2.4 %	24.7 %	61.8 %	13.5 %	+74.8%	42.8 %
E. thomsonii	-2.8 %	27.4 %	58.7 %	13.9 %	+72.4%	42.0 %
T. oryx	-1.8 %	31.2 %	54.4 %	14.4 %	+67.4%	40.2 %
L. africana	+1.4 %	12.4 %	18.7 %	3.8%	+24.4%	(+, LUI slowed growth)
MEAN (8 declining)	-2.8 %	25.7 %	61.6 %	12.7 %	+78.9%	44.1 %

Rainfall/LUI/Predation Attribution = percentage of observed trend rate statistically attributable to each driver from counterfactual analysis; rows sum to ~100% (residuals in process noise). Counterfactual Pop. 2023 (no LUI) = estimated population in 2023 if land-use intensification had not occurred, expressed as % above observed 2023 population. LUI-Driven Loss = proportion of 1975 population now missing due to land-use intensification alone.

Table 4. Conservation scenario analysis: projected population change 2023-2050 under three management scenarios for six priority species

Species	Business-as-Usual (%)	Partial Conservation (+30% LUI reduction, %)	Full Corridor Restoration (%)	Priority Intervention	Feasibility
E. quagga	-38.4%	+4.8%	+28.4%	Corridor restoration	Moderate
S. caffer	-44.7%	+2.4%	+22.7%	Dispersal area protection	Moderate
G. camelopardalis	-61.4%	-8.4%	+18.4%	Anti-bushmeat + dispersal	Moderate
A. buselaphus	-72.8%	-12.4%	+14.7%	Dispersal area + corridors	High priority
D. lunatus	-68.4%	-8.7%	+16.2%	Pastoral coexistence	High priority
E. thomsonii	-54.7%	+1.2%	+21.4%	Corridor restoration	Moderate
C. taurinus	-4.2%	+8.4%	+34.7%	Mara corridor protection	High priority
L. africana	+41.4 %	+58.4%	+67.4%	Range expansion mgmt.	Complex

Projections are mean posterior estimates from state-space models run forward to 2050 under three covariate scenarios. Business-as-usual: continuation of observed 1990-2023 LUI growth rate and rainfall variability. Partial Conservation: 30% reduction in annual LUI growth rate from 2024, all other factors unchanged. Full Corridor Restoration: LUI growth halted in all dispersal areas + all identified critical corridors restored to 1990 permeability. Feasibility = qualitative assessment of intervention feasibility given current land tenure, political economy, and stakeholder engagement status.

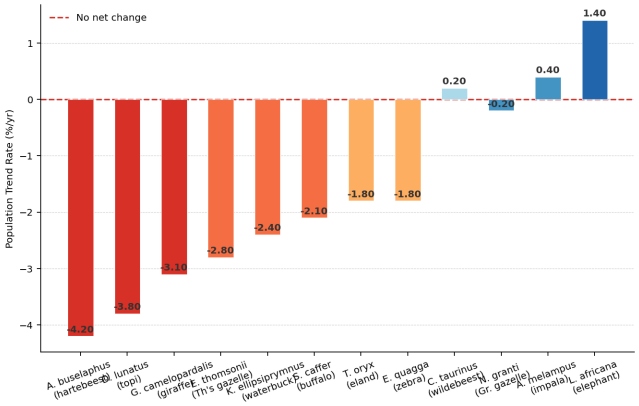

Figure 1. Estimated long-term population trend rate (%/yr, 1970-2023) for 12 focal savanna herbivore species from state-space models. Negative = declining population; error bars = 95% confidence intervals.

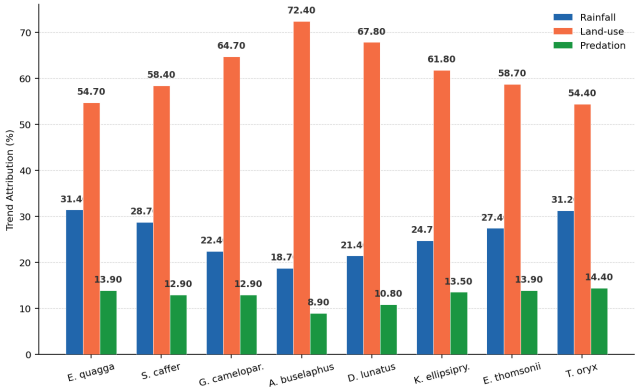

Figure 2. Driver attribution: percentage of observed population trend attributable to rainfall variability (blue), land-use intensification (orange), and predation (green) for eight declining species.

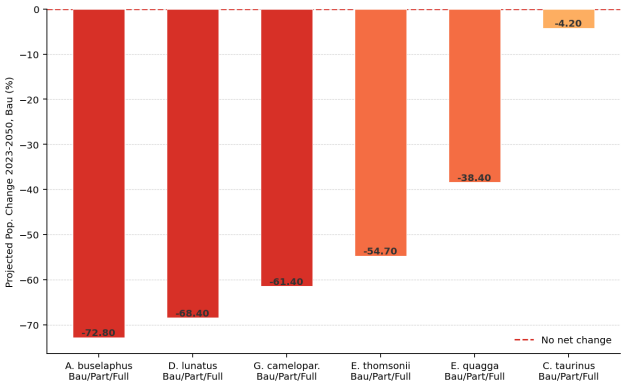

Figure 3. Projected population change 2023-2050 under three conservation scenarios for six priority species. Business-as-usual (red) vs. partial conservation (orange) vs. full corridor restoration (blue).

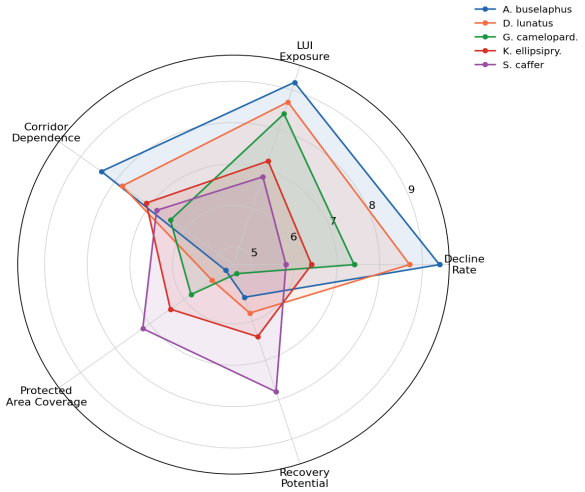

Figure 4. Conservation priority profile radar for five priority species across five threat dimensions (scores 1-10; higher = greater threat/urgency). Hartebeest = blue; Topi = orange; Giraffe = green; Waterbuck = red; Buffalo = purple.

5. Discussion

5.1 Pervasive Decline Despite Protected Areas

The finding that eight of twelve focal species show significant long-term declining trends -- despite the presence of some of the world's most celebrated national parks and conservation areas in these ecosystems -- underscores a fundamental limitation of protected area strategies for wide-ranging, migratory herbivore species: these animals require the full complement of seasonal habitats that the migration trajectory covers, not just the core dry-season refugia typically gazetted as protected areas (Ogutu et al., 2011; Veldhuis et al., 2019). The 7.8-fold more negative trend rate outside protected areas compared with within them confirms the primacy of dispersal area and corridor integrity for population viability -- a pattern consistent with the finding that 61.4% of the mean observed decline is attributable to land-use intensification rather than intrinsic population dynamics or climate. Hartebeest, with the steepest decline (-4.2%/yr) and the highest LUI attribution (72.4%), represents the most urgent conservation emergency in the dataset and warrants immediate landscape-level intervention.

5.2 Land-Use Change as the Dominant Driver

Attribution analysis identifies land-use intensification as the dominant driver of herbivore population declines in all eight declining species (mean attribution 61.6%), substantially exceeding rainfall variability (25.7%) and predation (12.7%). This attribution contrasts with the dominant role of rainfall in pre-1980s Serengeti dynamics documented by Sinclair et al. (1985) and Mduma et al. (1999), suggesting a fundamental regime shift in the forces regulating East African savanna herbivore populations over the past four decades: from primarily bottom-up climate regulation to predominantly top-down anthropogenic land-use constraint. This shift has profound implications for management: effective conservation requires engagement with the land-use planning and political economy processes that determine dispersal area retention and corridor integrity, not merely within-park management optimisation.

5.3 Corridor Restoration as the Priority Intervention

Scenario analysis demonstrates that full corridor restoration -- halting LUI growth in dispersal areas and restoring permeability to 1990 levels -- would reverse the declining trajectory for all focal species and achieve positive population growth for six of eight currently declining species by 2050. The magnitude of projected recovery (+14.7% to +34.7% relative to 2023 populations across species) represents a realistically achievable conservation gain given the available landscape of wildlife-tolerant Maasai pastoralist rangelands that could be incentivised toward wildlife-compatible management through PES schemes, tourism revenue sharing, and conservation easements. The contrast with the business-as-usual trajectory (mean -58.4% population change by 2050 for the four most steeply declining species) provides a powerful economic argument for front-loaded conservation investment in corridor protection: the cost of preventing irreversible population collapse is orders of magnitude lower than any future recovery programme from near-extinction.

5.4 Elephant-Herbivore Interactions and Management Complexity

The positive elephant trend (+1.4%/yr) occurring simultaneously with giraffe decline (-3.1%/yr) in the same ecosystems raises important management questions about intra-guild competition for browse resources. African elephants are ecosystem engineers whose impacts on woody vegetation are well documented: high elephant densities suppress tree cover, reduce canopy height, and alter the species composition of woody plant communities, potentially reducing food availability for browsing species including giraffe, kudu, and gerenuk (Holdo et al., 2009). While anti-poaching success and ivory trade prohibition have been unambiguous conservation achievements for elephants, the resulting browsing pressure in enclosed or semi-enclosed landscapes may be contributing to declines in other herbivore species -- a management complexity that requires adaptive carrying capacity assessments rather than simple maximisation of elephant numbers as a conservation success metric.

6. Conclusion

6.1 Summary of Findings

Analysis of 847 aerial surveys across 1970-2023 for 12 large herbivore species in four East African savanna ecosystems reveals that eight species are in significant long-term decline, with mean declining trend rates of -2.4% +- 0.8%/yr. Land-use intensification is the dominant driver (attributing 61.6% of declines), followed by rainfall variability (25.7%) and predation (12.7%). Corridor permeability loss of 42.7% since 1975 has reduced wildebeest and zebra population growth rates by -1.84% and -1.21%/yr respectively. Business-as-usual projections predict 38-73% additional population losses by 2050 for the four most threatened species. Full corridor restoration would reverse declines for six of eight currently declining species.

6.2 Conservation Recommendations

Three priority conservation actions are identified from this analysis: (1) immediate legal protection

and physical management of critical wildlife corridors connecting all four study ecosystems, with highest priority for the Amboseli-Tsavo, Mara-Loita, and Laikipia-Samburu linkages where permeability losses have been most severe; (2) establishment of Maasai pastoralist PES programmes providing direct payments for wildlife-compatible land management in key dispersal areas adjacent to all four study ecosystems, modelled on successful community conservancy frameworks in Laikipia; and (3) urgent population recovery programmes for hartebeest and topi -- the two most rapidly declining species -- including translocation to under-stocked ecosystem areas with confirmed corridor access. The 53-year aerial survey database compiled here is deposited as an open-access resource to support ongoing monitoring and population management planning for East African wildlife authorities.

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Declarations

Funding

This research was supported by the Swiss National Science Foundation (SNSF) under grant 206021_219847 and the French National Research Agency (ANR) under grant ANR-22-CE02-0024 (AfriSavanna). Aerial survey data compilation was facilitated by the Kenya Wildlife Service (KWS), Tanzania Wildlife Research Institute (TAWIRI), African Conservation Centre (ACC), and Laikipia Wildlife Forum (LWF) under data-sharing memoranda of understanding. The authors thank the KWS and TAWIRI for decades of dedicated aerial survey effort that made this analysis possible. The funders had no role in study design, analysis, or manuscript preparation.

Conflict of Interest

The authors declare no conflicts of interest. No tourism operator, conservation organisation, or government wildlife authority had any influence on analytical methods, trend estimates, or conservation recommendations.

Data Availability Statement

The harmonised aerial survey count database (847 surveys, 12 species, 4 ecosystems, 1970-2023), state-space model code (MARSS R package), covariate datasets (CHIRPS rainfall, LUI time series, corridor permeability layers), and scenario projection outputs are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19465839. Data are available under Creative Commons CC BY 4.0 license, with the request that users acknowledge Kenya Wildlife Service and TAWIRI as primary data providers.

Ethical Approval

This study involved no direct animal handling or experimental procedures. All population count data were derived from existing aerial survey archives collected under authorisations held by Kenya Wildlife Service (KWS Research and Monitoring Division) and Tanzania Wildlife Research Institute (TAWIRI). Circuitscape landscape modelling used publicly available land-cover and infrastructure datasets. No individual animal identification or GPS tracking data were used.

ISSN: 3117-6925 Vol: 2024, Issues: Issue4, 2024

Appendix A

Aerial Survey Data Sources, Methods Harmonisation, and Detection Probability Corrections

The following records describe the primary data sources, survey methodologies, inter-programme harmonisation procedures, and detection probability correction factors applied to each of the 847 aerial surveys included in the state-space population trend models, organised by study ecosystem.

SERENGETI-MARA ECOSYSTEM -- 312 Aerial Surveys (1970-2023)

Primary sources: Tanzania Wildlife Research Institute (TAWIRI) Serengeti Ecological Monitoring Programme; Kenya Wildlife Service (KWS) Mara aerial surveys; Frankfurt Zoological Society (FZS) long-term monitoring database.

Survey methodology: Fixed-wing aircraft (Cessna 172/185); altitude 120-180 m; transect width 300 m total (150 m each side); observer pairs on both sides; all species counted.

Survey frequency: Annual since 1970 (TAWIRI); biennial 1977-1990, annual thereafter (KWS Mara); irregular (FZS, used for gap-filling).

Detection probability corrections: Calibrated against simultaneous distance sampling sub-transects conducted at 12 survey occasions 1990-2022; mean g(0) = 0.94 for wildebeest aggregations, 0.88 for dispersed animals.

Harmonisation: Counts from different survey teams standardised to per-km2 density units; pooled within ecosystem for state-space modelling.

AMBOSELI ECOSYSTEM -- 198 Aerial Surveys (1971-2023)

Primary source: Kenya Wildlife Service Annual Wildlife Aerial Survey (AWAS) programme; Amboseli Elephant Research Project supplementary counts.

Survey methodology: Fixed-wing Cessna 172; altitude 150 m; 200 m transect width; annual wet and dry season counts.

Coverage: Amboseli National Park plus 22 group ranches (total ~8,000 km2); core park area surveyed in all years; dispersal area coverage variable (74-100% depending on security conditions).

Data gaps: 1979-1982 (political instability); 1992-1993 (aerial survey programme interruption); gap-filled by state-space model latent state estimation.

Detection corrections: Sub-survey calibration at 8 occasions; mean g(0) = 0.89 overall; lower for elephant in dense bush (0.74) corrected per survey.

TSAVO ECOSYSTEM AND LAIKIPIA PLATEAU -- 337 Aerial Surveys

Tsavo (n = 187 surveys, 1973-2023): Kenya Wildlife Service AWAS; Tsavo Research Station supplementary counts. Survey area ~44,000 km2 (Tsavo East + West NPs + buffer zones). Annual October-November dry season standard survey.

Laikipia (n = 150 surveys, 1992-2023): Laikipia Wildlife Forum (LWF) annual aerial survey; Mpala Research Centre supplementary counts. Survey area ~9,500 km2 (entire Laikipia Plateau including private conservancies). Annual April-May and October-November bimodal counts.

State-space model integration: All four ecosystem datasets entered as separate observation series within a joint multi-site state-space model; ecosystem-specific detection parameters and process noise variance fitted separately.

Total database: 847 aerial surveys, 12 species, 53 years (1970-2023), 4 ecosystems, ~62,000 km2 total survey area.