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RESEARCH ARTICLE

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Assessing protected area effectiveness in western Tanzania: Insights from repeated line transect surveys

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Abstract

In many parts of East Africa, wildlife populations have declined over the past decades. Given these trends, site-based studies are needed to assess how protected areas with differing management strategies enable the effective conservation of wildlife populations. In Tanzania, game reserves are managed for tourist hunting, while national parks are managed for non-consumptive wildlife-based tourism. To assess the relative performance of these management strategies, we here focus on two areas: Rukwa Game Reserve (RGR) and Katavi National Park (KNP). Based on systematically designed line distance surveys in 2004 and 2021, we compared densities and group sizes of large mammal populations (African elephant, giraffe, buffalo, zebra, topi, and hartebeest) over time. Contrary to published ecosystem-wide declines observed in numerous species which considered earlier baselines, we did not detect significant population declines between 2004 and 2021. While these new results showing apparent stable populations do not invalidate earlier studies on wildlife declines, they could indicate a stabilisation phase after declines. This highlights the importance of considering appropriate temporal baselines and historical contexts when assessing conservation effectiveness.

KEYWORDS
conservation evidence, declining population paradigm, ecological effectiveness, group size, shifting baseline syndrome, wildlife monitoring

Résumé

Dans de nombreuses régions de l'Afrique de l'Est, les populations d'animaux sauvages ont diminué au cours des dernières décennies. Compte tenu de ces tendances, des études sur le terrain sont nécessaires pour évaluer comment des zones protégées dotées de stratégies de gestion différentes permettent une conservation efficace des populations d'animaux sauvages. En Tanzanie, les réserves de chasse sont gérées pour la chasse touristique, tandis que les parcs nationaux sont gérés pour le tourisme non consommateur d'espèces sauvages. Pour évaluer la performance relative de ces stratégies de gestion, nous nous concentrons ici sur deux domaines : la Réserve de Chasse de Rukwa (RGR) et le Parc National de Katavi (KNP). Sur la base d'études systématiques de distance linéaire en 2004 et en 2021, nous avons comparé les densités et les tailles de groupe des populations de grands mammifères (éléphant d'Afrique, girafe, buffle, zèbre, topi et bubale) au fil du temps. Les tests Z ont indiqué qu'il n'y avait pas de différence considérable en matière de densité de toutes les espèces prises en compte entre les deux études. Contrairement aux publications sur les déclins à l'échelle de l'écosystème observés chez de nombreuses espèces qui ont pris en compte des données de référence antérieures, nous n'avons pas détecté de déclins considérables de la population entre 2004 et 2021. Si ces nouveaux résultats montrant une apparente stabilité des populations n'invalident pas les études antérieures sur le déclin des espèces sauvages, ils pourraient indiquer une phase de stabilisation après le déclin. Cela souligne qu'il est important de prendre en compte des bases temporelles et des contextes historiques appropriés au moment d'évaluer l'efficacité de la conservation.

1 | INTRODUCTION

Globally, wildlife populations have declined markedly over the past decades (WWF, 2022). East Africa is no exception to this worrisome trend: by 2005, an index of wildlife abundance had declined to about half of its 1970 baseline (Craigie et al., 2010). To date, protected areas (PAs) are the key conservation strategy to counteract wildlife population declines (Dinerstein et al., 2017; Geldmann et al., 2013; Naughton-Treves et al., 2005). These PAs are typically classified according to the International Union for Nature Conservation (IUCN) scheme (IUCN, 2008). In the context of Tanzania, national parks (NPs, IUCN category II; 22 areas with a total extent of 104,559 km^2; TANAPA, 2023) and game reserves (GRs, IUCN category VI; 25 areas with a total extent of 97,190 km^2; TAWA, 2023) are of outstanding relevance for maintaining wildlife populations as these two PA categories cover vast areas (Protected Planet, 2023) and typically harbour the greatest densities of wildlife populations (Stoner, Caro, Mduma, Mlingwa, Sabuni & Borner, 2007, Stoner, Caro, Mduma, Mlingwa, Sabuni, Borner & Schelten, 2007). National parks are managed in a way to minimise human pressures and restrict land use to non-consumptive tourism (i.e. wildlife watching) and research. Game reserves also largely exclude people. However, tourist hunting based on a quota system is permitted and used to generate income from these areas (Caro & Davenport, 2016). In a few Game Reserves, wildlife research is carried out (e.g. Wilfred & MacColl, 2016).

The current biodiversity crisis urgently calls for renewed wildlife monitoring efforts in PAs to provide the evidence basis for guiding conservation management (Cuadros et al., 2015; Ghoddousi et al., 2022; Kiffner et al., 2020). For multiple sites in Tanzania, and based on data from aerial wildlife surveys collected from the late 1980s to the early 2000s, Stoner, Caro, Mduma, Mlingwa, Sabuni & Borner (2007) and Stoner, Caro, Mduma, Mlingwa, Sabuni, Borner & Schelten (2007) found that wildlife populations inside NPs and GRs were generally faring better over time than in adjacent areas with fewer restrictions on land use. However, this assessment is nearly two decades old. Moreover, ongoing controversy over trophy hunting (e.g. Di Minin et al., 2016; Dickman et al., 2019; Ghasemi, 2021; Treves et al., 2019) calls for objective assessments of the long-term persistence of wildlife populations subject to such selective, yet perpetual consumptive use.

A robust and updated assessment of the ecological outcomes of PAs is particularly important for the Katavi-Rukwa Ecosystem of western Tanzania. Partially fuelled by immigration, this ecosystem has experienced substantial human population growth (Salerno et al., 2017); associated changes in land use (Giliba et al., 2022) and high rates of illegal wildlife hunting observed in this ecosystem (Martin & Caro, 2013) have been hypothesised to contribute to rapid wildlife population declines (Caro et al., 2013). Based on aerial survey data, several authors have observed ecosystem-wide declines in large herbivore species (Caro et al., 2013; Giliba et al., 2022; Mtui et al., 2017). Over a span of 27–37 years, aerial survey data revealed a non-significant negative trend in the elephant (*Loxodonta africana*) population and significant declines in populations of giraffe (*Giraffa camelopardalis tippelskirchi*), buffalo (*Syncerus caffer*), zebra (*Equus quagga*), topi (*Damaliscus lunatus*), and hartebeest (*Alcelaphus buselaphus*). These declines were largely corroborated by temporal trends of wildlife densities assessed through strip sampling along roads inside Katavi National Park over a 20-year time period (Caro, 2016). However, when analysing these shorter time series, the trend analyses only replicated the direction of the population trend, yet the *p*-value surpassed the 0.05 threshold (except for elephant and topi), leaving uncertainty regarding the existence of a definite trend (Caro, 2016).

While assessments of wildlife populations through aerial and vehicle-based surveys are valuable, they may be associated with possible biases that limit the resulting inferences. For example, aerial surveys tend to underestimate the density of smaller species and even large-bodied species such as giraffes (Greene et al., 2017;

Lee & Bond, 2016). In addition, vehicle-based surveys may introduce bias if transects are non-randomly distributed and follow roads (Kiffner et al., 2022; Marques et al., 2013). Importantly, since the road transect surveys ended in 2015 (Caro, 2016) and the last aerial survey was conducted in 2018 (Giliba et al., 2022), updated estimates are required to better understand population trends in the ecosystem.

To provide such updated estimates, we conducted line transect surveys along systematically distributed sampling units in the two key protected areas – Katavi National Park (hereafter KNP) and Rukwa Game Reserve (hereafter RGR) – in 2021, using a similar transect layout and comparable field protocols to a wildlife survey carried out in 2004 (Waltert et al., 2008, 2009). Our aim was to test whether populations of six large herbivore species have declined over an 18-year period in the Katavi-Rukwa Ecosystem.

Assuming a decline in these herbivore populations is not only based on the previously cited publications on wildlife declines in the ecosystem but also founded on documented anthropogenic changes over the past decades. In the year prior to the 2004 ground survey, farmers built a dam upstream of the Katuma river, thereby substantially reducing water influx to KNP (Caro et al., 2013). Over the past three decades, and especially over the past two decades, areas outside of the core protected areas have experienced substantial land cover changes with woodlands being converted to croplands; in several locations, cropland is now directly bordering protected areas (Giliba et al., 2022). Alongside land use changes, reported incidences of crop raiding and livestock losses due to wildlife are frequent in the ecosystem (Hariohay et al., 2017). Moreover, illegal hunting for meat is prevalent (Mgawe et al., 2012), whereby hunters opportunistically harvest herbivore species, including all species considered in this analysis (Martin et al., 2013). Available evidence suggests that pressure arising from illegal hunting increased from 1994 to 2012 (Caro et al., 2013). While "bushmeat" hunters in the Katavi-Rukwa Ecosystem rarely hunt elephants, targeted illegal hunting of elephants, often organised by transnational syndicates, also occurs in the ecosystem (Jones et al., 2018; Martin & Caro, 2013). Globally, illegal ivory trade reached high levels between the two time intervals. Therefore, elephant poaching in the study system was assumed to be high between the two survey periods, especially between 2010 and 2015 (Kideghesho, 2016; Schlossberg et al., 2020; Wasser et al., 2015). In sum, these anthropogenic pressures negatively impact large mammal populations, but a knowledge gap exists in how far these impacts might have further deteriorated wildlife populations in the target area for the period between 2004 and 2021.

We fill this knowledge gap by comparing (1) estimated densities and (2) observed group sizes between the two surveys. While density comparisons provide a direct test of population-level changes over time, group sizes are sensitive to human exploitation and may thus serve as an additional indicator for human-induced changes in wildlife populations across time or space (e.g. smaller group sizes in RGR vs. KNP; Caro, 1999a). Finally, and to avoid falling into the shifting baseline syndrome trap (Pauly, 1995), we discuss our findings in the context of previous research on wildlife population trends carried out in this ecosystem.

2 | MATERIALS AND METHODS

2.1 | Study area

The study sites, KNP and the adjacent RGR, are located in southwestern Tanzania and form the central part of the Katavi-Rukwa Ecosystem. Both PAs are situated in and around the Rukwa depression, which is connected to the Great Rift Valley (Scoon, 2018). The area experiences a unimodal rainfall pattern with average annual precipitation ranging from 800 mm in lower elevations to 1000 mm in higher elevations (TANAPA/WD, 2004). The ecosystem falls within the Central Zambezi miombo woodlands ecoregion (Burgess et al., 2004; Rodgers, 1979). However, the species-rich tree community is dominated by *Terminalia sericea*, *Combretum adenogonium*, and *C. colinum*, a species composition that is atypical of the miombo biome (which is typically characterised by *Brachystegia* spp. and *Julbernadia* spp. trees; Banda et al., 2008).

Katavi National Park was established in 1974 and now covers 4279 km^2 of mixed woodlands and seasonal floodplains. The park is almost exclusively situated within the Rukwa depression at altitudes between 800 and 1100 m. The park is famous for its high densities of large terrestrial mammals (Caro, 1999b) and large aggregations of hippopotamus (*Hippopotamus amphibius*) around the Katuma River and the two seasonal lakes, Lake Katavi and Lake Chada (Caro et al., 2013; Lewison & Carter, 2004). Tanzania National Parks (TANAPA) manages KNP and rangers patrol the area. According to its designation as NP, land use is restricted to research and non-consumptive wildlife tourism; tourist numbers are low, especially when compared to other Tanzanian NPs in the North of the country.

Rukwa Game Reserve was established in 1961 and now covers 4323 km^2 at altitudes ranging from 800 to 1600 m. The higher elevations, i.e. plateaux and hills, are part of the northern escarpment of the Great Rift Valley (Scoon, 2018). Floodplains are mostly limited to areas bordering Lake Rukwa and woodland areas are more predominant compared to KNP (Waltert et al., 2009). In 2004, RGR was managed by the Wildlife Division (WD); since 2016, this authority has been restructured and is since labelled Tanzania Wildlife Management Authority (TAWA). This change in the authority's name did not change the designation of the area and on-the-ground management. Staff of RGR patrol the area and oversee tourist hunting operations, which are allowed in designated hunting blocks. Hunting operators operate multiple camps in RGR and hunting off-take is based on a quota system (Kiffner et al., 2009; Waltert et al., 2009). Hunting is exclusively permitted during the time period spanning from July to the end of November. Law enforcement is carried out by RGR staff. As far as we are aware, no comprehensive evaluations have been conducted to assess the efficacy of law enforcement measures in either of the PAs. However, findings from the 2004 survey indicated a greater occurrence of illegal activities in RGR compared to KNP (Waltert et al., 2009).

2.2 | Sampling design and field protocols

In 2004 and 2021, we used systematically distributed line transects to collect data of six large herbivore species (elephant, giraffe, buffalo, zebra, topi, and hartebeest). These species can easily be detected, are relatively abundant species in mammal communities of Miombo woodlands (Rodgers, 1979), and have declined significantly (either based on aerial or vehicle transects) over the past decades (Caro, 2016). During both surveys, we walked along systematically distributed triangular-shaped line transects to assess wildlife populations (Figure 1). Triangular transects are advantageous because they have the same start and end point, thus easing logistics of fieldwork.

In 2004, transect layout was based on a systematic 9×9 km grid and each triangle leg was 4 km in length (i.e. 12 km transect length). If triangles overlapped protected areas, we assigned sections of the transect to the corresponding protected area. We attempted to sample all 105 transects; however, due to inaccessibility, we could only sample a total of 87 transects: 44 in KNP and 43 in RGR. Because the 2021 survey did not cover the eastern part of RGR, we omitted data from 27 transects of the 2004 survey (thus considering 26 transects) to obtain a more similar spatial coverage for our comparison. Total line length was 829.0 km: 523.2 km in KNP and 305.8 km in RGR (Table 1). More details of the 2004 survey are outlined in Waltert et al. (2008).

In 2021, transect layout was based on systematic random sampling and a 5×5 km grid. The grid was centred on KNP and included adjacent areas within 35 km of KNP; therefore the eastern part of RGR was not sampled in 2021. In both KNP and RGR, we randomly selected 21 transects. Each triangle leg was 1 km in length (i.e., 3 km transect length). During the 2021 survey, none of the transects overlapped with protected area boundaries. Total line length was 126 km: 63 km in each PA (Table 1).

Fieldwork of both surveys was carried out during the dry season: from August through September 2004 and from July through September 2021. Moreover, we attempted to keep the sampling protocol as similar as possible across surveys. Despite the differences in personnel between the two survey periods, the consistent adherence to a standardised sampling protocol was ensured through prior training. During each survey, three trained persons walked along the transect with one person mostly in charge of navigation

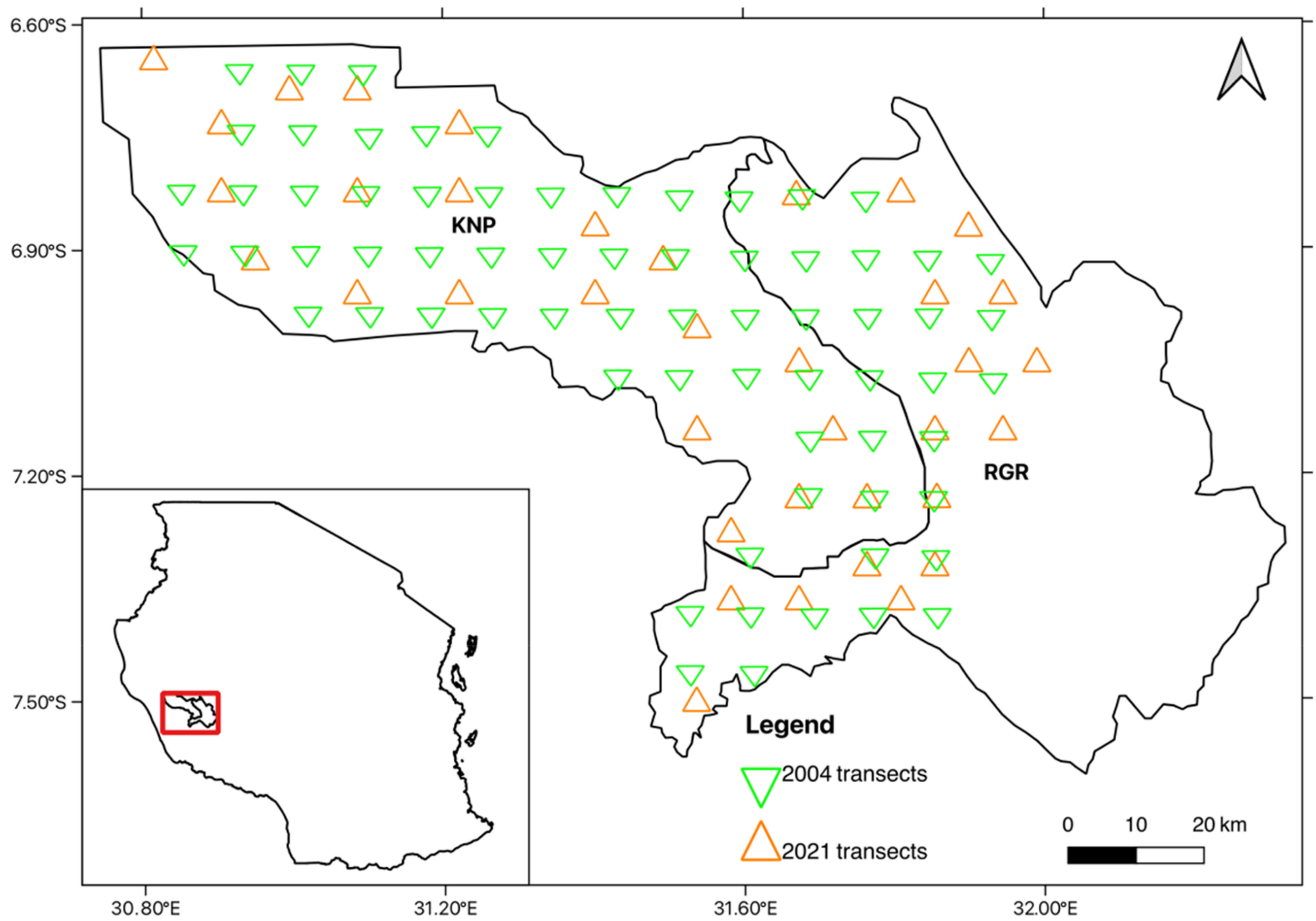

FIGURE 1 Map of Katavi National Park (KNP) and Rukwa Game Reserve (RGR) showing the transect design in 2004 and 2021. The inset in the lower left shows the location of the study site within Tanzania. For visualisation purposes, transects are not to scale.

TABLE 1 Summary of line transect surveys carried out in the two protected areas (PA) Katavi National Park (KNP) and Rukwa Game Reserve (RGR) in 2004 and 2021; n_d, the number of detections during each survey; n_t, the number of transects; L, the sum of km walked per survey; ER, the encounter rate (n_d/L; after truncating 10% of the data) incl. associated 95% confidence intervals.

Species	Year	PA	n_d	n_t	L	ER (95% confidence intervals)
Elephant	2004	KNP	26	44	523.2	0.04 (0.02; 0.08)
Elephant	2021	KNP	7	21	63.0	0.11 (0.05; 0.24)
Elephant	2004	RGR	3	26	305.8	0.01 (0.00; 0.03)
Elephant	2021	RGR	6	21	63.0	0.10 (0.02; 0.44)
Giraffe	2004	KNP	42	44	523.2	0.06 (0.04; 0.10)
Giraffe	2021	KNP	26	21	63.0	0.41 (0.16; 1.10)
Giraffe	2004	RGR	8	26	305.8	0.03 (0.01; 0.06)
Giraffe	2021	RGR	3	21	63.0	0.05 (0.01; 0.27)
Buffalo	2004	KNP	21	44	523.2	0.03 (0.02; 0.06)
Buffalo	2021	KNP	11	21	63.0	0.17 (0.07; 0.44)
Buffalo	2004	RGR	3	26	305.8	0.01 (0.00; 0.04)
Buffalo	2021	RGR	2	21	63.0	0.03 (0.01; 0.12)
Zebra	2004	KNP	59	44	523.2	0.10 (0.05; 0.21)
Zebra	2021	KNP	12	21	63.0	0.19 (0.08; 0.43)
Zebra	2004	RGR	4	26	305.8	0.01 (0.00; 0.03)
Zebra	2021	RGR	0	21	63.0	0
Topi	2004	KNP	37	44	523.2	0.06 (0.04; 0.11)
Topi	2021	KNP	2	21	63.0	0.03 (0.01; 0.12)
Topi	2004	RGR	0	26	305.8	0
Topi	2021	RGR	0	21	63.0	0
Hartebeest	2004	KNP	4	44	523.2	0.01 (0.00–0.02)
Hartebeest	2021	KNP	5	21	63.0	0.08 (0.03; 0.21)
Hartebeest	2004	RGR	8	26	305.8	0.02 (0.01; 0.06)
Hartebeest	2021	RGR	3	21	63.0	0.05 (0.02; 0.14)

(using handheld GPS units), one person mainly responsible for spotting animals and one person recording data.

Upon encountering wildlife, observers identified the observed wildlife to species level, and counted the group size of the sighting (defined as individuals of the same species within ca. 50 m, a commonly used threshold for defining groups of terrestrial herbivores; Kasozi & Montgomery, 2020). In 2004, estimation of perpendicular distances was based on measuring sighting angles α with sighting compasses (SILVA sighting compass) and sighting distances r using laser range finders (LEICA LRF 900) and subsequent trigonometric calculation [$x = r$ sin (bearing-α)] to calculate perpendicular distances x (Waltert et al., 2008). In 2021, we measured perpendicular distances directly in the field, using a laser range finder (Nikon Prostaff 1000). Prior to fieldwork in 2004 and 2021, we trained observers in field methods (i.e. use of GPS navigation, use of rangefinder and sighting compass). During training, we emphasised key points to meet the main distance sampling assumptions. This included measuring to the centre of the group, accurately measuring distances, and accurately counting individuals in one group (Buckland et al., 2001).

2.3 | Data analysis

For both survey periods, the number of detections per species and per study area was relatively low (Table 1), and we therefore pooled detections to fit detection models (Buckland et al., 2001; Thomas et al., 2010). To account for possible differences in detectability across surveys and areas, we fitted four different models, each with a half normal key function (Gonzalez et al., 2017) and cosine extension: (1) a conventional distance sampling model, (2) a model with "Area" (KNP vs. RGR) as covariate for the detection process, (3) a model with "Year" (2004 vs. 2021) as covariate, and (4) a model with "Area" and "Year" as covariate. In all models, we discarded the furthest 10% of observations and modelled cluster sizes as the mean of observed, stratum-specific cluster sizes. As criterion for model selection, we used the sample-sized corrected Akaike's Information Criterion (AIC) score (Table 2). To compare the estimated densities between the 2004 and 2021 surveys, we used a z-test (Buckland et al., 2001).

In addition, we compared group sizes between 2004 and 2021, using generalised linear models with negative binomial error distribution, implemented via the *countreg* package (Zeileis et al., 2008) in the

R 4.13 environment (R Core Team, 2021). We chose this error distribution because group sizes are counts that showed signs of overdispersion. For each of the six species separately, we modelled the group size as a function of the survey year (2021 vs. 2004), the PA (RGR vs. KNP) and the interaction between the survey year and the PA. For zebra, we did not include the interaction term because no zebra were detected during the 2021 survey in RGR. For topi, we only tested for a year effect because all sightings were restricted to KNP (Table 1).

3 | RESULTS

During both survey periods and protected areas combined, we most frequently encountered giraffes ($n=79$ encounters), followed by zebra ($n=75$), elephant ($n=42$), buffalo ($n=37$), topi ($n=39$), and hartebeest ($n=20$; Table 1).

According to the sample size-corrected AIC scores, the detection process for elephant, giraffe, buffalo, and zebra was best modelled by including" Year" as covariate. In 2004, observers included sightings at further distances, whereas in 2021, observers rarely detected species beyond 100 m (Figure 2a–h). However, for topi and hartebeest, there was little support to include covariates to describe the detection process (Table 2). Indicated by visual assessments of the fitted function (Figure 2) and test statistics of the Kolmogorov–Smirnov test (elephant model $p=0.621$; giraffe model $p=0.602$; buffalo model $p=0.528$; topi model $p=0.303$; hartebeest model $p=0.986$), the selected models showed good fit. Only the zebra model ($p=0.006$) did not fit well, most likely due to a slight heaping of observations at 500 m (Figure 2g).

Based on the selected detection functions, we estimated area- and year-specific densities. Overall, species-specific densities remained fairly similar over time (Figure 3). Indeed, *z*-tests did not reveal any significant differences in pairwise density comparisons (Table 3). While the density of topi appeared to have declined between 2004 and 2021 (Figure 3e), a *z*-test did not detect a significant signal ($p=0.08$; Table 3).

In all six species, average group sizes were significantly ($p<0.05$) smaller in 2021 compared to 2004 (Figure 4 and Table 4). However, the assumption that group sizes of giraffe, buffalo, zebra, or hartebeest were generally smaller in RGR compared to KNP was not supported ($p>0.07$; Table 4). Contrary to our initial assumption, we found that elephant group sizes were greater in RGR compared to KNP. We did not detect a strong signal for a 'protected area × year' interaction in any of the single-species models.

4 | DISCUSSION

To assess long-term population trajectories of six large mammalian herbivores (African elephant, giraffe, buffalo, zebra, topi, and hartebeest) in KNP and RGR, we conducted systematically distributed line distance surveys in 2004 and 2021 and compared estimated densities and observed group sizes between survey periods.

TABLE 2 Sample size corrected AIC scores for species-specific detection models for conventional detection models without covariate, and for models with either "Area", "Year" or "Area and Year" as covariate for the detection process. Most supported models are italicized.

Covariate	Species	AICc	Δ AICc
None	Elephant	408.32	9.00
Area	Elephant	411.16	11.84
Year	*Elephant*	*399.32*	*0.00*
Area and Year	Elephant	400.79	1.47
None	Giraffe	708.79	30.12
Area	Giraffe	717.09	38.42
Year	*Giraffe*	*678.67*	*0.00*
Area and Year	Giraffe	680.73	2.06
None	Buffalo	366.88	9.75
Area	Buffalo	374.70	17.57
Year	*Buffalo*	*357.13*	*0.00*
Area and Year	Buffalo	359.41	2.28
None	Zebra	790.64	10.69
Area	Zebra	809.46	29.51
Year	*Zebra*	*779.95*	*0.00*
Area and Year	Zebra	781.89	1.93
None	*Topi*	*421.20*	*0.00*
Area	Topi	429.64	8.44
Year	Topi	422.40	1.20
Area and Year	Topi	422.40	1.20
None	*Hartbeeest*	*158.94*	*0.00*
Area	Hartbeeest	161.41	2.47
Year	Hartbeeest	161.04	2.10
Area and Year	Hartbeeest	160.82	1.88

Despite reported significant wildlife declines assessed via aerial surveys (Caro, 2016; Caro et al., 2013; Giliba et al., 2022) and similar, yet not always statistically significant trends derived from road transect data (Caro, 2016), our data did not provide substantial evidence for widespread population declines between 2004 and 2021. However, our repeated ground-based line transect surveys suggest that group sizes of several species may have declined between 2004 and 2021.

4.1 | Did group sizes change between 2004 and 2021?

Across species and the two PAs, our data provided relatively consistent support for smaller group sizes in 2021 compared to 2004 (Figure 4 and Table 4). Estimating group size is an integral part of population size assessments. Moreover, animals adjust group size adaptively to cope with variation in natural or anthropogenic predation risk, resource availability, social factors, with fitness-relevant implications (Bond et al., 2019; Creel et al., 2014; Krause & Ruxton, 2002;

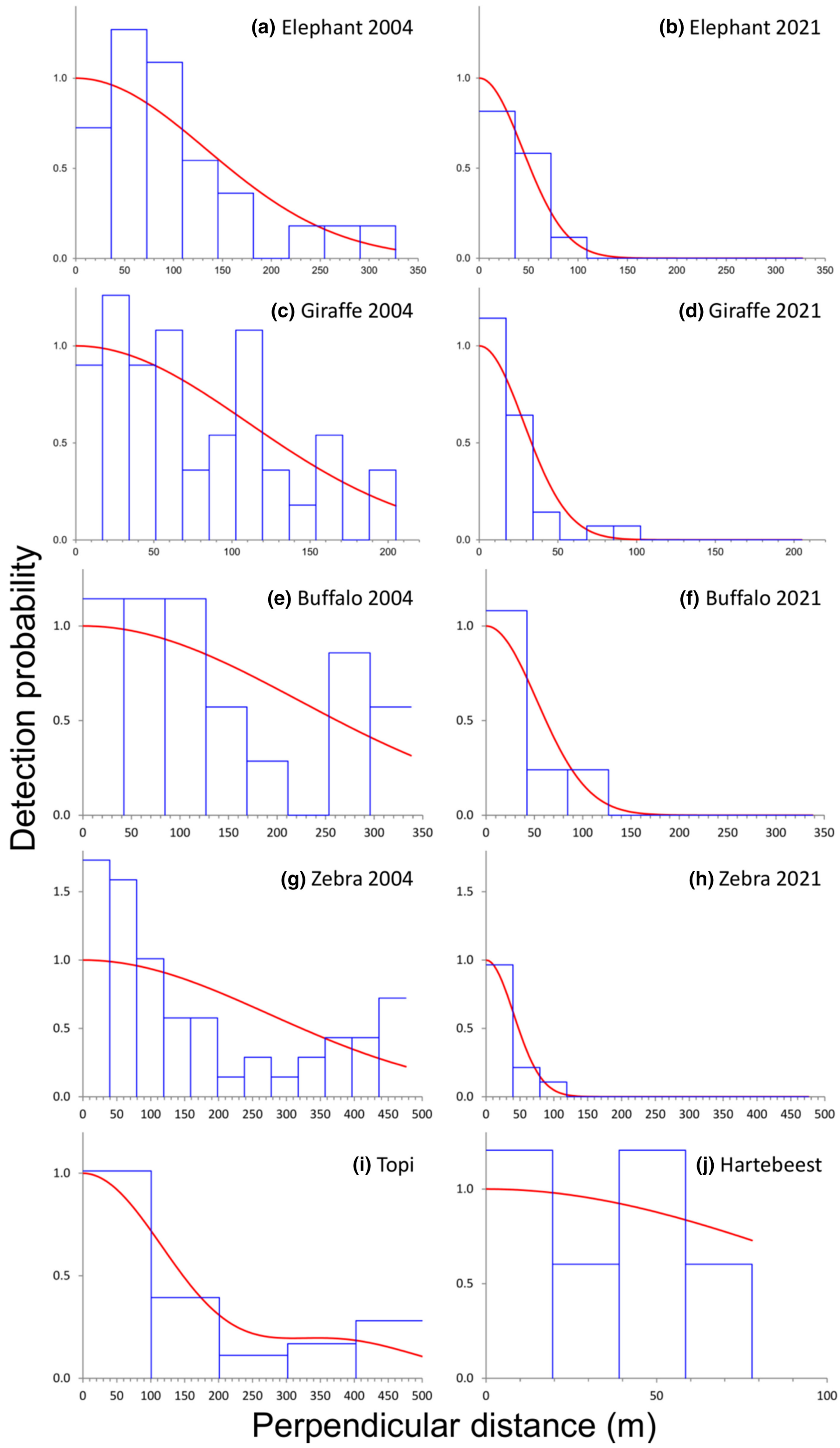

FIGURE 2 Frequency of sightings per distance bin (blue histogram) and fitted detection function (red line) for six large herbivores detected along line transects in Katavi National Park (KNP) and Rukwa Game Reserve (RGR) in 2004 and in 2021. If incorporating "Year" as covariate for the detection process was supported (Table 2), we plotted the detection function for each factor combination.

Leweri et al., 2022). While a detailed analysis to assess fine-scaled correlates of group sizes would go beyond the scope of this manuscript, we also caution against attaching too much importance to the apparent decline in group sizes. Our caution stems from the fact that sample sizes for 2021 were relatively small (Table 1) and that we modelled average group sizes (Brennan et al., 2015). As group size distributions are typically right-skewed with most observations occurring at relatively small group sizes and only a few observations of large group sizes (Reiczigel et al., 2008; also evident in Figure 4), a small sample size reduces the chances of detecting larger groups. As larger group sizes (e.g., large buffalo herds comprising several hundred individuals or large aggregations of topi, Figure 4) strongly influence mean group size values, failure to detect such large groups due to low sampling effort would substantially lower average group sizes.

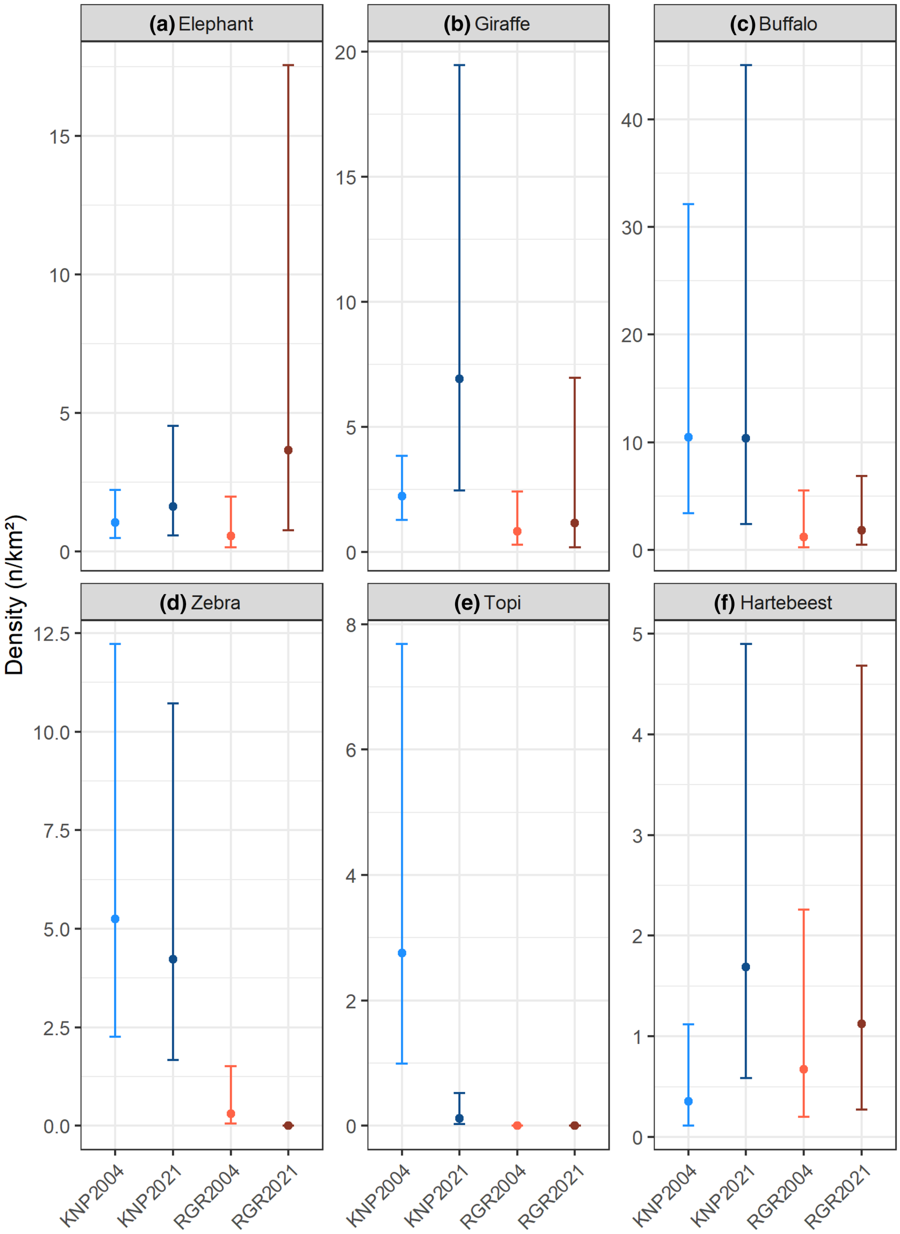

FIGURE 3 Estimated densities (n/km^2) of (a) elephant, (b) giraffes, (c) buffalo, (d) zebra, (e) topi, and (f) hartebeest for line transect surveys in Katavi National Park (KNP) and Rukwa Game Reserve (RGR) in 2004 and in 2021. Error bars indicate 95% confidence intervals.

4.2 | Did wildlife populations decline between 2004 and 2021?

To account for the relative small sample sizes, we pooled detections across surveys and modelled detection functions with covariates (Thomas et al., 2010). While sample sizes were below the recommended thresholds for modelling of detection functions (Buckland et al., 2001), the chosen detection function fitted the data reasonably well (Figure 2) and allowed estimating animal densities while accounting for differences in the detection process between the two survey periods. Overall, our approach did not detect significant declines in any of the six considered species.

While none of the comparisons yielded a significant signal, possible exceptions to the apparent stable population densities may have been the topic in KNP, which showed both a significant decline in group sizes (Figure 4e) and an apparent, though non-significant decline in densities (Figure 3e). For this species, both road-based transect surveys and systematic aerial surveys also documented a declining population trend (Caro, 2016). Another exception may be zebra, which have not been sighted directly during the 2021 survey in RGR. However, zebra dung was frequently detected while walking along transects, suggesting that this species persisted in RGR as well (R. A. Giliba, C. Kiffner, P. Fust, & J. Loos, in review).

Although the overall pattern of stable population densities of the considered species seems like good news for wildlife conservation in the Katavi-Rukwa Ecosystem, these results seemingly contradict previously published data on widespread wildlife population declines in the ecosystem (Caro, 2011, 2016; Caro et al., 2013; Giliba et al., 2022). Multiple, mutually non-exclusive hypotheses could explain these apparent discrepancies. One explanation involves the timing of the surveys. Recent analyses of PA- and species-specific wildlife data obtained from aerial surveys highlight non-linear

TABLE 3 Estimated species-, area-, and survey-specific densities for six large herbivores in Katavi National Park (KNP) and Rukwa Game Reserve (RGR).

		2004		2021			
Species	**Area**	**D**	**CV**	**D**	**CV**	***z*-Value**	***p*-Value (two-tailed)**
Elephant	KNP	1.03	39.66	1.62	53.39	−0.61	0.541
Elephant	RGR	0.55	67.28	3.65	88.69	−0.95	0.342
Giraffe	KNP	2.22	28.19	6.91	53.90	−1.24	0.214
Giraffe	RGR	0.82	56.94	1.15	106.14	−0.26	0.798
Buffalo	KNP	10.48	59.46	10.37	80.92	0.01	0.991
Buffalo	RGR	1.19	85.24	1.82	71.43	−0.38	0.705
Zebra	KNP	5.25	44.34	4.22	48.40	0.33	0.739
Zebra	RGR	0.30	79.71	0.00	0.00	1.25	0.209
Topi	KNP	2.75	55.11	0.12	78.96	1.73	0.083
Topi	RGR	0.00		0.00			
Hartebeest	KNP	0.35	62.81	1.69	55.93	−1.38	0.169
Hartebeest	RGR	0.67	65.60	1.13	74.01	−0.48	0.631

Note: *z*-values and associated two-tailed *p*-values refer to tests between the two survey periods.

wildlife declines, with major downward trends observed during the 1990s (Giliba et al., 2022). The use of different baselines may have influenced contrasting findings of significant and non-significant population trends (Mihoub et al., 2017): while Caro (2016) used baselines from the 1980s or 1990s, our study used data from the year 2004 as a baseline. Thus, our data do not necessarily refute the overall notion that wildlife populations have declined in the ecosystem. While there is clear evidence for historic declines in the considered species across the ecosystem (Caro, 2011, 2016; Caro et al., 2013; Giliba et al., 2022), our data suggest that these species did not further decline between 2004 and 2021. More generally, considering appropriate temporal baselines and the historical context is crucial for estimating conservation effectiveness. Relying solely on a single, relatively recent baseline may obscure the true extent of wildlife population declines in the ecosystems (i.e. the shifting baseline syndrome; Pauly, 1995). Incorporating historical data and long-term trends into conservation assessments provides a more robust foundation for understanding the true impact, or absence thereof, of conservation efforts. This approach serves as an antidote to the shifting baseline syndrome, a phenomenon where each generation perceives the degraded state of the environment as the "new normal" (Papworth et al., 2009). It enables the assessment of the magnitude of changes, and determination of whether the current state of wildlife populations aligns with historical baselines or represents a concerning departure from them. Consequently, achieving the goal of restoring wildlife populations to historical baselines would require much more effective conservation actions than those currently employed (Prins & de Jong, 2022).

Alternatively, it could be that wildlife populations declined beyond the year 2004 but perhaps rebounded at least partially after Caro's data collection ended in 2015 (Caro, 2016). However, aerial survey data from a dry season 2018 survey carried out by the "Tanzania Wildlife Research Institute" (TAWIRI, 2018) provide only some indication that buffalo in game reserves may have rebounded slightly. Based on aerial surveys, other species do not seem to have recovered during the last few years (Figure 4 in Giliba et al., 2022). In sum, these considerations broadly suggest that – for the considered time period – populations of elephant, giraffe, buffalo, and hartebeest have remained fairly stable, whereas topi and zebra showed signs of continued population decline. Nonetheless, compared to baselines from the 1970s, current densities of all target species are much lower (Giliba et al., 2022).

Finally, the lack of statistically significant differences in population densities between 2004 and 2021 could indicate low test power. The coefficients of variation observed in both surveys were relatively large: in 2004, coefficients of variation averaged 58% (range: 28%–85%) and in 2021 they averaged 65 (range: 48%–106%). Consequently, detecting "significant" differences would require substantial density differences to be present between the two periods (Andersen & Steidl, 2020). To address this issue and to improve precision would require increasing the sampling efforts or implementing stratification techniques, but these options may impose additional financial burdens on wildlife surveys (Waltert et al., 2008).

4.3 | Towards sustainable wildlife conservation in the Katavi-Rukwa ecosystem

The persistence of all considered wildlife species and the apparent stable (considering the 2004–2021 time period) population densities of the considered large herbivore species are likely attributable to the remarkable resilience of these species and dedicated conservation efforts in the Katavi-Rukwa Ecosystem. In between the two surveys, Tanzanian authorities targeted illegal elephant hunting activities and effectively persecuted multiple transnational ivory poaching and trafficking syndicates, thereby reducing illegal hunting of elephants (Alden & Harvey, 2021). Nevertheless, illegal hunting is

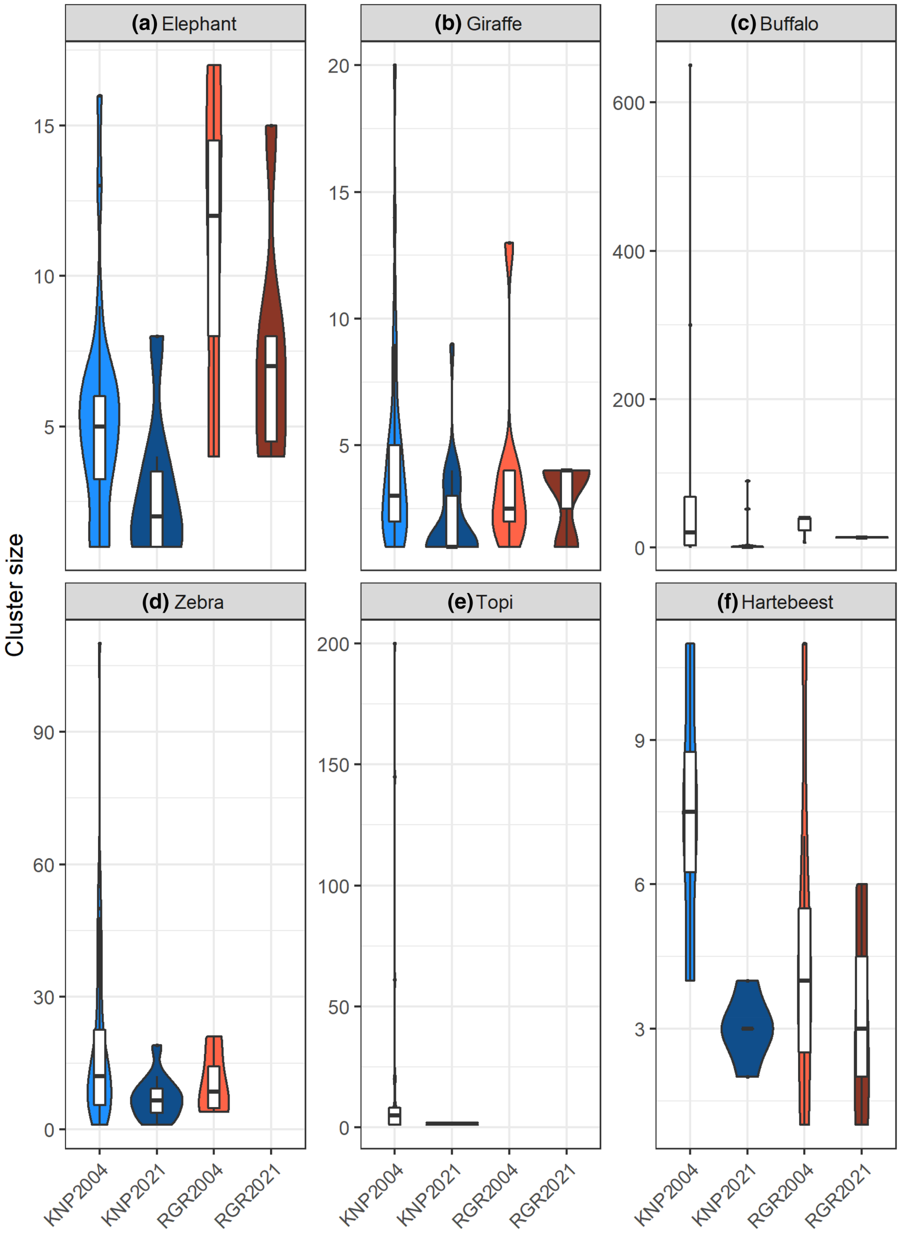

FIGURE 4 Distribution of group sizes of (a) elephant, (b) giraffes, (c) buffalo, (d) zebra, (e) topi, and (f) hartebeest counted along line transects in Katavi National Park (KNP) and Rukwa Game Reserve (RGR) in 2004 and 2021. The midpoint of the boxplot indicates the median, and the box indicates the middle 50% of group sizes and whiskers indicate the first and fourth quartiles.

likely still a major issue in the ecosystem, requiring holistic solutions beyond mere law enforcement (Fitzherbert et al., 2014; Martin & Caro, 2013; Mgawe et al., 2012).

Our data also indicate that legal trophy hunting may contribute to the maintenance of wildlife in the ecosystem. Large herbivore densities in RGR were mostly lower compared to corresponding densities in KNP (Figure 3; see Caro, 1999a, 1999b; Waltert et al., 2008). This pattern of lower densities in GRs compared to NPs is consistent across multiple comparisons in Tanzania (Stoner, Caro, Mduma, Mlingwa, Sabuni & Borner, 2007, Stoner, Caro, Mduma, Mlingwa, Sabuni, Borner & Schelten, 2007). In the case of the density differences observed in KNP and GR, these differences may, however, largely be due to variation in habitat structure (greater proportion of grasslands in KNP compared to the more wooded RGR) and unlikely due to the fact that the monitored species (except for giraffe which cannot be hunted legally in Tanzania) are legally hunted (Waltert et al., 2009). Although our data do not allow more detailed analysis of the sustainability of trophy hunting (Crosmary et al., 2013; Milner et al., 2007; Muposhi et al., 2015), our data suggest that long-term persistence of large herbivore population in trophy hunting areas is possible. Due to the lack of detailed information on hunting off-take, we recommend to continue wildlife monitoring and undertake more targeted and comprehensive research to assess the sustainability of trophy hunting.

Beyond pressures due to direct exploitation of wildlife, the ecosystem currently faces massive land use changes, with agriculture encroaching upon PA boundaries (Giliba et al., 2022). Converting woodlands to agriculture compresses wildlife populations further inside core areas of the existing PAs, reduces effective habitat area and blocks remaining wildlife corridors. To secure the ecological integrity of the Katavi-Rukwa Ecosystem, either by conserving the current status of wildlife populations or possibly by restoring wildlife

TABLE 4 Coefficient estimates of species-specific regression models with negative binomial error distribution, testing the effect of protected area [PA: Rukwa Game Reserve (RGR) vs. Katavi National Park (KNP)], year (2004 vs. 2021), and the interaction between protected area and year on group sizes of elephant, giraffe, buffalo zebra, topi, and hartebeest.

	Estimate	Std. error	*z*-Value	*p*-Value
Elephant				
Intercept	1.66	0.12	13.87	<0.01
Year (2021 vs. 2004)	−0.61	0.30	−2.03	0.04
PA (RGR vs. KNP)	0.74	0.33	2.26	0.02
PA × Year (2021 × RGR)	0.23	0.48	0.47	0.64
Giraffe				
Intercept	1.46	0.11	13.00	<0.01
Year (2021 vs. 2004)	−0.73	0.21	−3.54	<0.01
PA (RGR vs. KNP)	−0.11	0.29	−0.37	0.71
PA × Year (2021 × RGR)	0.47	0.57	0.83	0.40
Buffalo				
Intercept	4.33	0.33	13.18	<0.01
Year (2021 vs. 2004)	−1.69	0.57	−2.99	<0.01
PA (RGR vs. KNP)	−0.98	0.93	−1.05	0.30
PA × Year (2021 × RGR)	0.94	1.50	0.63	0.53
Zebra				
Intercept	2.90	0.11	26.43	<0.01
Year (2021 vs. 2004)	−0.92	0.28	−3.29	<0.01
PA (RGR vs. KNP)	−0.55	0.45	−1.23	0.22
Topi				
Intercept	2.79	0.23	12.17	<0.01
Year (2021 vs. 2004)	−2.39	1.15	−2.07	0.04
Hartebeest				
Intercept	2.01	0.22	9.31	<0.01
Year (2021 vs. 2004)	−0.92	0.35	−2.60	0.01
PA (RGR vs. KNP)	−0.51	0.29	−1.79	0.07
PA × Year (2021 × RGR)	0.62	0.53	1.17	0.24

populations to historic baselines (i.e. densities observed during the 1970s or even earlier time periods) likely requires an integrated approach that equally considers the needs of people and those of wildlife (Fischer et al., 2021). Importantly such efforts require renewed investments in robust and long-term monitoring schemes which allow linking wildlife population trends to anthropogenic and environmental drivers of wildlife population dynamics (Caro et al., 2013; Caughley, 1994).

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CONFLICT OF INTEREST STATEMENT

The authors have no financial or personal relationships with any individuals or organisations that could inappropriately influence or bias the content of this paper.

DATA AVAILABILITY STATEMENT

The data are not publicly available as they include sensitive information on the spatial distribution of wildlife species, but they can be obtained upon reasonable request.

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