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Using density surface models to assess the ecological effectiveness of a protected area network in Tanzania

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Abstract

Given recent global endeavors to increase protected area coverage, it is crucial to comprehensively evaluate the efficacy of various area-based conservation strategies in effectively reducing biodiversity loss. Here, we investigated the responses of wildlife populations to different protection levels and environmental variables at the landscape scale in the Katavi–Rukwa Ecosystem, western Tanzania. To this end, we conducted line distance sampling surveys and counted the dung of six target mammal species (elephant, giraffe, buffalo, zebra, topi, and hartebeest) along foot transects within areas differing in protection levels (from strict to less-strictly protected: national park, game reserve, forest reserve, game-controlled area, and unprotected areas). Based on these dung counts, we modeled the spatial distribution of these six mammal species using a species-specific density surface modeling framework. We found consistent effects of protection level and land use variables on the spatial distribution of the target mammal species: dung densities were highest in the national park and game reserves, intermediate in less-strictly protected areas, and lowest in unprotected areas. Beyond species-specific environmental predictors for dung densities, our results highlight consistent negative associations between dung densities of the target species and distance to cropland and avoidance of areas in proximity to houses. Our findings underpin differences in ecological effectiveness of protected areas within one ecosystem. Protection level and land use play crucial roles in moderating the spatial distribution of all considered mammal species. Our findings suggest that a landscape approach needs to guide effective conservation across the entire protection gradient of the Katavi–Rukwa Ecosystem.

KEYWORDS
conservation effectiveness, conservation evidence, distance sampling, Miombo, protected and conserved areas, spatial distribution models

INTRODUCTION

In a global context, large mammals are facing rapid declines due to multiple anthropogenic pressures (Geldmann et al., 2014, 2019; Ripple et al., 2015). Most large mammal populations on the African continent (Craigie et al., 2010; WCMC-UNEP, 2016) and in Tanzania (Stoner et al., 2007) are no exceptions to this worrying global trend. To respond to increasing human pressures, protected and conserved areas (PCAs) have become a primary approach for safeguarding biodiversity including large mammals (CBD, 2022; IPBES, 2019; Justin Nowakowski et al., 2023).

PCAs in Tanzania vary in their protection levels, ranging from strictly protected (IUCN Categories I–V) to less-strictly protected, permitting human activities and resource extraction to some extent (IUCN Category V; Caro & Davenport, 2016). However, their effectiveness in protecting large mammals and natural habitat is challenged, mostly because of (1) direct exploitation and habitat degradation inside protected areas, and (2) increasing isolation through habitat loss and other anthropogenic pressures in the wider landscape in which the PCAs are embedded (Caro, 2008; Giliba et al., 2022, 2023; Lobora et al., 2018; Martin et al., 2013; Newmark, 1996). Thus, it is crucial to evaluate the effectiveness of different levels of area-based protection, not only by monitoring wildlife within PCAs, but also by quantifying wildlife populations in the wider landscape.

Through spatially explicit information on wildlife densities, it may be possible to determine the effectiveness of the PCA network from a landscape perspective. However, assessing the ecological effectiveness of PCAs based on average wildlife densities at a single point in time, without accounting for environmental variables, presents a significant challenge. This is because environmental conditions, which may primarily determine the carrying capacity of a given species (e.g., Pettorelli et al., 2009), vary between PCAs (Rosenblatt et al., 2016, 2019). Thus, it is necessary to disentangle whether differences in wildlife densities are due to inherent differences in environmental conditions or due to specific area-based conservation efforts (Waltert et al., 2009).

While a suite of wildlife detection methods are available, wildlife surveys are typically labor- and cost-intensive, or are difficult to implement over large spatial scales (Jachmann, 1991, 2002; Schwarz & Seber, 1999; Williams & Nichols, 2002). Over the past 30 years, aerial counts have been widely used in wildlife monitoring within the Katavi–Rukwa Ecosystem (Caro, 2016; Giliba et al., 2022; Stoner et al., 2007). Although this method has the ability to cover large and remote areas, the estimates derived from aerial counts are typically lower than estimates from ground counts due to sighting and visibility bias (Greene et al., 2017; Jachmann, 1991, 2002). To overcome potential biases associated with aerial surveys, terrestrial line surveys have been suggested for wildlife monitoring and applied within the study region to estimate wildlife densities across different protected areas (Caro, 1999a, 1999b). These surveys bear the great advantage to provide fine-scale data to unravel species distribution and habitat use, but often, these surveys are being conducted along the existing road network, and this nonrandom placement of sample units may yield biased density estimates (Kiffner et al., 2022; Waltert et al., 2008).

To address the shortcomings of systematic aerial surveys and road counts, foot counts along systematically distributed transects have been used to estimate wildlife populations in Katavi National Park (KNP) and Rukwa Game Reserve (RGR) (Waltert et al., 2008). Yet, this survey method yielded sufficient number of detections for few species only: despite more than 1000 km of walking transect effort, only four species were detected more than 60 times (Waltert et al., 2008), which is the recommended threshold for estimating robust detection functions in a line distance sampling framework (Buckland et al., 2001; Thomas et al., 2010).

The low detection rates from direct counts could be partially due to animal behavior, which itself can be mediated by protection level. For instance, animals may be indifferent toward human observers inside strictly PCAs but skittish (and thus less likely to be detected) in less strictly in PCAs where legal or illegal hunting takes place (Caro, 2005). Such hunting impacts some species directly, while other species might be affected more indirectly. In addition, species may adjust their temporal use of certain areas and use human-dominated areas primarily during nighttime (de Jonge et al., 2022; Gaynor et al., 2018). Thus, relying on direct sightings during daytime to estimate wildlife density along a protection gradient could be biased due to variation in animal behavior. A solution for such scenarios is the use of indirect survey methods such as dung surveys (Jachmann, 1991; Kiffner et al., 2019).

To address these challenges, we conducted a comprehensive study to quantify wildlife densities using a spatially explicit density surface modeling (DSM) framework (Miller et al., 2013), combining data from a systematic dung survey and remotely sensed information. Our choice to focus on dung densities stemmed from the challenges in approximating absolute densities from dung density estimates, as this would mandate detailed estimations of defecation rates and the dung decay rates (Ahrestani et al., 2018; Lunt et al., 2007; Marques et al., 2001)—parameters that were not available for the target species in our study area. As such, dung density was harnessed as a proxy, providing a comparative lens for assessing animal density. Our research centered on six numerically dominant, large mammal species of the

Miombo biome (Caro, 1999a, 2008): buffalo *Syncerus caffer*, elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, hartebeest *Alcelaphus buselaphus*, topi *Damaliscus lunatus*, and zebra *Equus burchellii*. These species can be monitored with a relative degree of reliability through indirect ground surveys.

While the anticipation of higher dung densities of target species in strictly protected areas may not be unexpected, our study introduces novelty by accounting for environmental conditions that could influence species-specific densities. Furthermore, it innovatively combines spatially explicit information on the distribution of selected mammal species. Collectively, our research provides the foundational evidence for comparing the ecological effectiveness of a PCA network within the Miombo biome.

METHODS

Study area

Our study area is located in the Katavi–Rukwa Ecosystem in western Tanzania, covering ~20,961 km² and containing PCAs with different designations. The study

area lies between 6°–7° S and 30°–31° E (Figure 1) and is characterized by a mosaic of unprotected areas (UAs, i.e., land that does not have a formal conservation category), and formally protected areas. Protection levels range from areas with little enforcement of human land use restrictions (game-controlled areas [GCAs]: here, settlement, agriculture, and livestock keeping are not allowed, but hunting on permit in specific hunting blocks is allowed), areas that allow regulated resource extractions such as forest reserves (FR, here, limited timber and non-timber products extraction is permitted) and game reserves (GR, here, tourist game hunting on permit is allowed) to strictly protected national parks (NPs) where human activities are restricted to photographic tourism and research (Caro, 1999a; Caro & Davenport, 2016). The study area includes multiple PCAs, and we centered this study around KNP, the adjacent RGR, Lwafi Game Reserve (LGR), Mlele Game Controlled Area (GCA), Mpanda Line Forest Reserve, Msaginia Forest Reserve (MFR), and Nkamba Forest Reserve (NFR) (Figure 1).

The Katavi–Rukwa Ecosystem receives an annual rainfall between 800 and 1200 mm, while the temperature ranges between 17 and 26°C. Elevation ranges from 600 to 1800 m above sea level. The soil types range
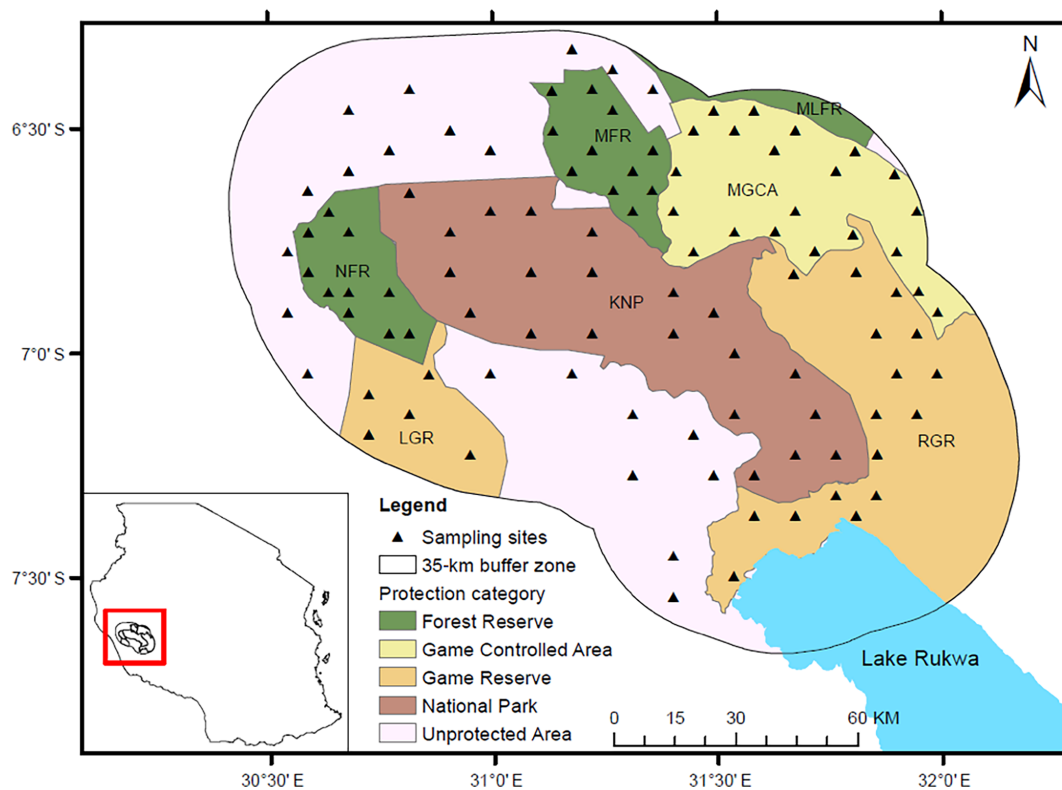

FIGURE 1 Map of the study area, highlighting the spatial distribution of wildlife dung sampling sites (triangular transects with three sections of 1-km length each) across protection levels (KNP, Katavi National Park; LGR, Lwafi Game Reserve; MFR, Msaginia Forest Reserve; MGCA, Mlele Game Controlled Area; MLFR, Mpanda Line Forest Reserve; NFR, Nkamba Forest Reserve; RGR, Rukwa Game Reserve). The inset in the lower left shows the location of the study area within Tanzania, with the red area marking the transect walks navigation.

from alluvial soils (black cotton soils) in flood plains to loamy soils in areas that are not seasonally inundated. The vegetation consists of Miombo woodlands in non-inundated areas and grasslands in the flood plains (Banda et al., 2006). Miombo forms a single story, with open canopy of deciduous woodland dominated by trees of the genera *Brachystegia, Julbernadia*, and *Isoberlinia* (Campbell, 1996). The human population in the Katavi–Rukwa Ecosystem has grown considerably due to immigration of pastoralist from other regions over the past 40 years (Izumi, 2017; Salerno, 2016) and due to general population increase in Tanzania. Agriculture and livestock keeping are the main land use activities (Caro, 1999a). Rice farming is restricted to river terraces and flood plains, while shifting cultivation for other crops such as maize, cotton, and tobacco is practiced in areas in which natural vegetation had previously been cleared (Giliba et al., 2022; Jew et al., 2015).

Field survey

We established a 35-km buffer around the boundary of the KNP to include areas with different protection levels, ranging from unprotected to strictly protected. To capture an even coverage of transects across different protection levels, we divided the study area into 5 × 5 km grids, so that transects were separated by 5 km to minimize spatial autocorrelation of the data. We randomly selected 105 grids

(21 grids within each protection level) and placed triangular-shaped transects of 3-km total length in the center of each selected grid. To ease logistics in the field (see Waltert et al., 2008), we opted for 1-km segment length (Figure 1). We surveyed each transect once during the dry season between July and September 2021. We acknowledge that this provides only one snapshot in time. However, as dung decay is relatively slow during the dry season (Boafo et al., 2008; Masunga et al., 2006), dung surveys integrate the distribution of large herbivores over a relatively long time span (i.e., at least several weeks).

Three people (one each primarily responsible for navigating, observing, and recording) walked along the transect. We used a handheld GPS and compass to navigate between segments (i.e., we moved toward 90° E in the first segment, 330° NW in the second segment, and 210° SW in the third segment; Figure 1). In each transect, we counted and recorded the number of individual dung piles of target species. Upon detection, we identified each dung pile to species level. To measure perpendicular distances from the center of a dung pile to the center line of a transect, we used a tape measure. To define the center line of the transect (and avoid rounding of distances near the line to zero), we placed a walking stick in the center of our path (Marques et al., 2001). Before the formal survey, we conducted a literature review and a pilot survey to establish species-specific dung pile definitions based on the shape of pellets and quantity of pellets per dung pile (Table 1). While this pilot study greatly helped

T A B L E 1 Attributes used to define individual dung piles for each target species based on number/pile and shape of pellets in the Katavi–Rukwa Ecosystem, western Tanzania.

Species	Sample size	No. pellets/pile				SE	Pellet shape
		Minimum	Maximum	Median	Mean		
Buffalo	12	1	2	1	1.16	0.11	Thick pancake-like pellets, very variable size and structure (Stuart & Stuart, 2019).
Elephant	12	3	6	4	4.42	0.28	Large barrel-shaped pellets (over 10 cm in diameter) accumulate in large dung heaps or partially broken up (Stuart & Stuart, 2019).
Giraffe	12	109	185	145	148.83	7.68	Roughly spherical pellets usually in scattered heaps, pellets pointed at one end (Stuart & Stuart, 2019).
Hartebeest	12	107	226	171	162.67	12.44	Roughly spherical or cylindrical commonly in heaps, pellets pointed at one end, diameter is relatively wider compared to topi (Hibert et al., 2008).
Topi	12	103	216	153	154.25	10.28	Roughly spherical or cylindrical commonly in heaps, pellets pointed at one end, diameter is relatively smaller compared to hartebeest (Hibert et al., 2008).
Zebra	12	10	32	22	22.67	2.12	Several separate kidney-like shape pellets with central vertical groove (Stuart & Stuart, 2019).

dung identification to species level in the field, we used animal tracks as additional hints to help with species identification. Despite due diligence and in the absence of DNA-based identification of dung (e.g., Bowkett et al., 2009), we cannot exclude the possibility that some misidentification occurred.

Estimating dung densities

We analyzed the data in a DSM framework, a two-stage method that first accounts for uncertain detectability (primarily as a function of distance between transect and observations; Thomas et al., 2010) and a spatial model of the density of the target population (Miller et al., 2013).

We used the function "ds" in the R package "distance" (Miller, 2022) to fit species-specific global detection functions. Due to low sample sizes per PCA level, we pooled species-specific sightings of dung piles across all

protection levels to fit global detection functions (Thomas et al., 2010). We truncated the farthest 10% of observations (Buckland et al., 2001) and fitted three models for each species: (1) half-normal with no adjustment terms, (2) uniform with cosine adjustment, and (3) hazard rate with cosine adjustment (Table 2). For all six species, we selected the half-normal function due to formal fit criteria (high chi-squared goodness-of-fit value), low Akaike information criterion values (Table 3), adequate visual fit (Figure 2), and evidence that half-normal detection functions typically yield unbiased estimates (Prieto Gonzalez et al., 2017).

Density surface modeling

To model the spatial distribution of the dung densities of the six target species, we used the function "dsm" in the R package "density surface modeling (DSM)" (Miller et al., 2022).

T A B L E 2 Key parameters associated with different detection models for dung of six target species.

Model	Truncation distance (%)	GOF p	Average detectability	SE of average detectability	ΔAIC
Buffalo					
Half-normal	10	0.058	0.632	0.030	0.000
Uniform	10	0.064	0.619	0.025	0.001
Hazard rate	10	0.073	0.590	0.050	2.985
Elephant					
Half-normal	10	0.063	0.758	0.036	0.000
Uniform	10	0.060	0.729	0.036	0.278
Hazard rate	10	0.071	0.723	0.061	2.891
Giraffe					
Half-normal	10	0.064	0.580	0.030	0.000
Hazard rate	10	0.092	0.517	0.042	0.806
Uniform	10	0.064	0.578	0.023	2.405
Hartebeest					
Uniform	10	0.049	0.737	0.041	0.000
Half-normal	10	0.052	0.773	0.041	1.414
Hazard rate	10	0.050	0.798	0.056	3.235
Topi					
Hazard rate	10	0.001	0.026	0.006	0.000
Uniform	10	0.067	0.648	0.065	13.825
Half-normal	10	0.059	0.679	0.071	15.497
Zebra					
Uniform	10	0.070	0.602	0.027	0.000
Half-normal	10	0.064	0.610	0.033	0.707
Hazard rate	10	0.078	0.602	0.054	1.892

Note: Dung counts were conducted on foot along systematically distributed transects in the Katavi–Rukwa Ecosystem, western Tanzania. GOF stands for chi-squared goodness of fit.

Abbreviation: AIC, Akaike information criterion.

TABLE 3 Parameter estimates of density surface models (parameterized as general additive models) to describe dung densities of target species across protection levels while accounting for environmental variables in the Katavi–Rukwa Ecosystem, western Tanzania.

Parametric variable	Estimate	SE	t	p	Smooth term	df	F	p
Buffalo								
Intercept	−3.472	0.1815	−19.127	<0.001***	Distance to cropland	4.158	3.004	<0.001***
Protection level GR	−1.136	0.3584	−3.170	0.002**	Distance to houses	4.927	3.476	<0.001***
Protection level GCA	−2.149	0.504	−4.263	<0.001***	Elevation	4.007	2.303	<0.001***
Protection level FR	−1.153	0.2758	−4.180	<0.001***	EVI	1.506	0.584	0.019*
Protection level UA	−87.92	6,980,000	0.000	0.999	Slope	2.104	1.18	0.001**
					Distance to rivers	2.156	0.805	0.011*
Elephant								
Intercept	−3.724	0.089	−41.892	<0.001***	Distance to cropland	0.800	0.439	0.023*
Protection level GR	0.174	0.115	1.522	0.129	Distance to houses	4.929	4.109	<0.001***
Protection level GCA	−0.218	0.242	−0.899	0.369	Distance to rivers	0.861	0.435	0.024*
Protection level FR	−0.534	0.184	−2.907	0.004**	Slope	0.775	0.366	0.034*
Protection level UA	−1.013	0.279	−3.632	<0.001***				
Giraffe								
Intercept	−3.433	0.101	−34.159	<0.001***	Distance to cropland	1.882	1.144	0.002**
Protection level GR	−0.432	0.173	−2.495	0.013*	Rainfall	2.388	0.703	0.040*
Protection level GCA	−0.827	0.307	−2.696	0.007**	EVI	1.887	0.742	0.018*
Protection level FR	−0.271	0.252	−1.077	0.282	Distance to rivers	0.931	1.470	<0.001**
Protection level UA	−86.140	6,992,000	0.000	0.999				
Hartebeest								
Intercept	−3.205	0.114	−28.003	<0.001***	Distance to houses	2.524	1.620	<0.001***
Protection level GR	0.026	0.150	0.173	0.863	EVI	1.037	0.350	0.047*
Protection level GCA	−0.406	0.190	−2.136	0.033*	Distance to rivers	1.893	1.199	0.001**
Protection level FR	−0.051	0.178	−0.287	0.774				
Protection level UA	−2.791	0.588	−4.748	<0.001***				
Topi								
Intercept	−4.475	0.250	−17.894	<0.001***	Distance to houses	3.197	1.709	0.020*
Protection level GR	−0.827	0.406	−2.034	0.043*	EVI	1.200	0.528	<0.001***
Protection level GCA	−0.653	0.425	−1.538	0.125				
Protection level FR	−0.758	0.364	−2.084	0.038*				
Protection level UA	−68.460	7,136,000	0.000	0.999				
Zebra								
Intercept	−3.712	0.111	−33.401	<0.001***	Distance to cropland	0.750	0.324	0.044*
Protection level GR	−0.268	0.184	−1.460	0.145	Distance rivers	1.984	0.983	0.006**
Protection level GCA	−1.150	0.304	−3.789	<0.001***	Slope	2.176	1.164	0.004**
Protection level FR	−0.624	0.280	−2.225	0.027*				
Protection level UA	−81.770	6,997,000	0.000	0.990				

Note: Protection level was defined as factor, whereas the baseline variable is national park.

Abbreviations: EVI, Enhanced Vegetation Index; FR, forest reserve; GCA, game-controlled area; GR, game reserve; NP, national park; UA, unprotected area.

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

In a first step, based on hypothesized relationships between the distribution of large savanna mammals in Tanzanian ecosystems and landscape features (Bond et al., 2017; Giliba et al., 2022, 2023; Van de Perre et al., 2014), we selected the following landscape variables for our spatially explicit models: the five-level categorical variable
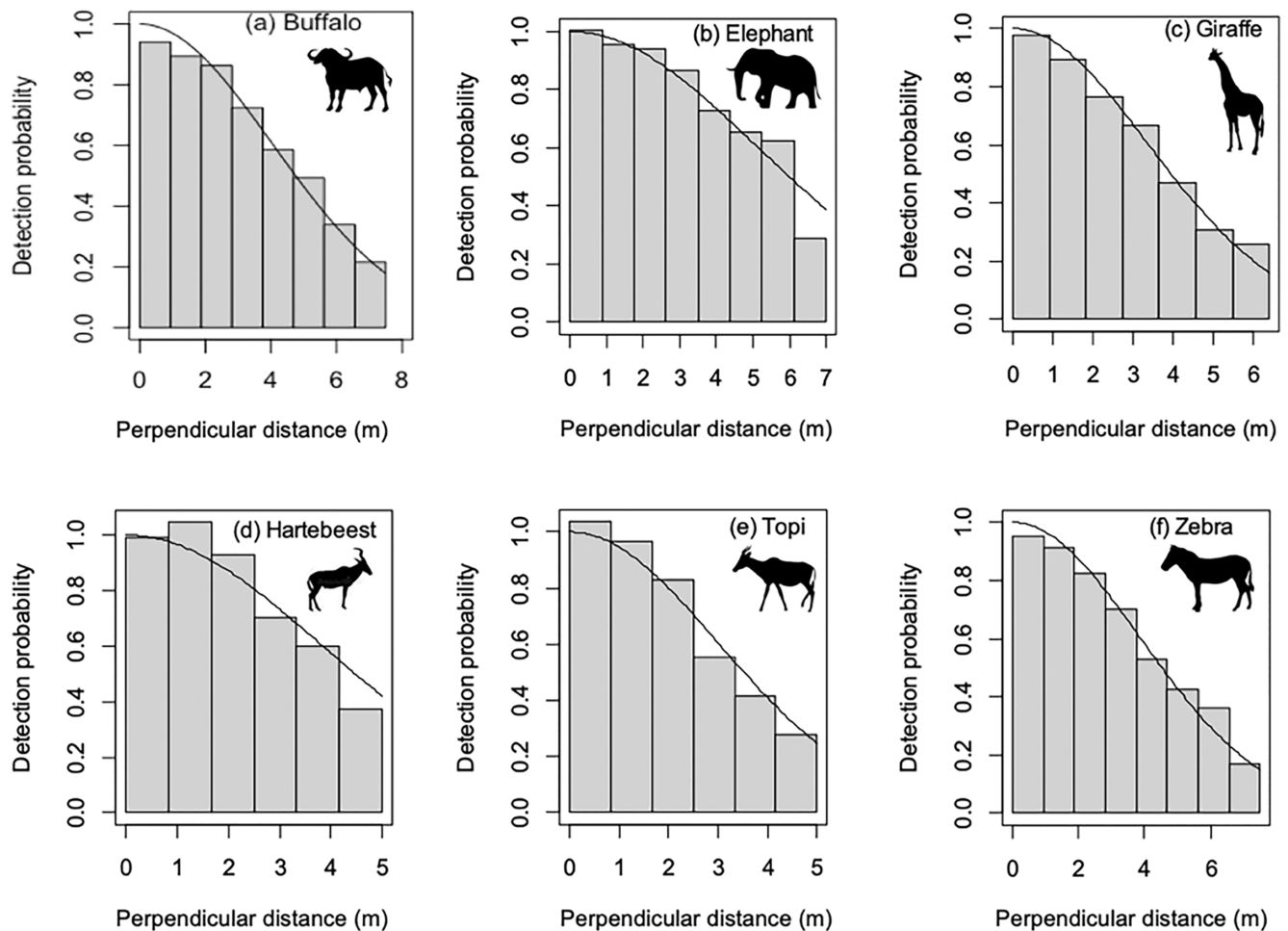
FIGURE 2 Detection functions (black line) of conventional distance sampling models for (a) buffalo, (b) elephant, (c) giraffe, (d) hartebeest, (e) topi, and (f) zebra sighted along foot transects in the Katavi–Rukwa Ecosystem in western Tanzania. The histograms (gray bars) show the observed frequency of dung sightings against perpendicular distance; detection functions (black lines) were modeled using half-normal key functions.

protection level, and the following numerical variables to account for environmental heterogeneity: elevation, slope, rainfall, distance to cropland, houses, rivers, and Enhanced Vegetation Index (EVI). We choose EVI as a proxy for primary productivity due to its advantages of reducing the background noise, atmospheric noise, and saturation in most cases compared with normalized difference vegetation index (Huete et al., 2002). We extracted elevation and slope data from SRTM digital elevation model from the U.S. Geological Survey (https://earthexplorer.usgs.gov) and annual rainfall data from CHIRPS (https://data.chc.ucsb.edu/products/CHIRPS-2.0/), using ArcMap 10.6 (ESRI, 2018). We quantified proximity to rivers and houses from spatial features obtained from OpenStreetMap (http://download.geofabrik.de/africa/tanzania.html), and proximity to cropland from 2021 land cover map generated by Giliba et al. (2022) in ArcMap 10.6 (ESRI, 2018), and EVI from Google Earth Engine—Landsat 8 Collection 1 Tier 1 8-Day EVI

Composite (Gorelick et al., 2017). Prior to modeling, all spatial layers were resampled to a 1-km resolution to overlap with our transects of 1-km segment length in ArcMap 10.6 (ESRI, 2018). Moreover, all numerical explanatory variables were scaled to mean zero and unit variance and tested for collinearity. For model fitting, we retained all variables because none of the variable dyads exceeded the $(r) \geq 0.7$ (Pearson's correlation coefficient) threshold (Dormann et al., 2013). We then prepared the segment data (table with sample label identifier for the segments, effort/length of segment, and the landscape variables), observation data (table with unique object identifier, sample label identifier for the segment where observation occurred, dung counts and distance to observations), and prediction data (a table/grid with all the potential landscape variables for prediction). In a third step, we modeled species-specific density and spatial distribution as a sum of spline smooth functions for the selected landscape variables using generalized additive models with Tweedie

family (Miller et al., 2013; Wood, 2017). This probability distribution is able to deal with zero-inflated data (Peel et al., 2013; Strindberg et al., 2018), a prerequisite for our data that contained many transects without any sightings, particularly in UAs. We used the stepwise backward selection procedure for variable selection ($p > 0.05$ as criteria for removing nonsignificant variables) within generalized additive models (Marra & Wood, 2011).

RESULTS

After controlling for associations with fine-scaled environmental (i.e., distance to rivers, elevation, EVI, rainfall, slope) and anthropogenic (i.e., distance to houses, distance to cropland, protection level) variables at a 1-km resolution, our density surface models consistently indicated a positive correlation between protection level and species-specific dung densities. Dung densities were highest in the NP for buffalo, giraffe, topi, and zebra, as well as in GR for elephant and hartebeest, whereas UAs consistently exhibited the lowest densities across all target species (Table 3).

For buffalo, the density surface model demonstrated that buffalo dung densities increased with greater distances from cropland and rivers. Additionally, they exhibited positive associations with EVI and slope, while elevation and distance to houses showed hump-shaped relationships with buffalo dung densities (Appendix S1: Figure S1a). Similarly, elephant dung densities increased with greater distances from cropland and rivers, displayed a negative association with slope, and showed a hump-shaped relationship with distance to houses (Appendix S1: Figure S1b). For giraffes, the model indicated that dung densities increased with greater distance from cropland and rivers, while they were negatively associated with precipitation and exhibited a hump-shaped curve with EVI (Appendix S1: Figure S1c). Hartebeest dung densities increased with greater distance to houses and rivers, but decreased with EVI (Appendix S1: Figure S1d). Dung densities of topi decreased with increasing EVI and showed a hump-shaped association with distance to houses (Appendix S1: Figure S1e). Finally, the density surface model for zebras showed that dung densities increased with greater distances to cropland, displayed a positive association with slope, and decreased with greater distances from rivers (Appendix S1: Figure S1f).

DISCUSSION

Our study is one of few recent empirical attempts to model densities of terrestrial wildlife species across different protection levels and across a large spatial extent (but see Maisels et al., 2013; Strindberg et al., 2018). While accounting for environmental variables, our model provides quantitative evidence on the effectiveness of area-based conservation measures for large mammal populations in a sub-Saharan African context. In particular, we quantify, within a Miombo ecosystem in western Tanzania, the extent to which areas subjected to a stricter protection level exhibited higher dung densities of large mammals compared with areas with less stringent protection levels or those that are unprotected. Our findings support conclusions from previous studies in the same (Caro, 1999a; Giliba et al., 2022) and other Tanzanian ecosystems (Kiffner et al., 2020; Oberosler et al., 2020) that UAs are less effective in supporting viable population densities of large mammal species.

Generally, all considered species were widely distributed in strictly protected areas (especially KNP but also GR) compared with less-strictly protected areas (Figure 3a–f), suggesting that the protection level largely explains the spatial distribution of large mammals in the Katavi–Rukwa Ecosystem. These findings confirm the strong influence of the protection level in regulating distributions and densities of large mammals in East Africa (Bhola et al., 2012; Kiffner et al., 2020). As our study is correlative in nature, we can merely speculate on the underlying, mutually nonexclusive, mechanisms for the positive impact of strict, area-based conservation management on wildlife populations in this ecosystem: stricter protection could (1) result in lower human-caused mortality either due to legal (in GR and GCAs) and/or illegal hunting (all PCAs), given effective implementation (Waltert et al., 2009); (2) lead to better habitat quality due to better protection from habitat degradation compared with less-strictly protected areas given adequate species and habitat management (Schwartz et al., 2002). In addition, (3) stricter PCAs could have an inherently greater carrying capacity for the target species that could not be explained by the selected environmental variables. However, these increased ecological outcomes are subject to adequate conservation funding and good governance.

While these findings indicate the ecological effectiveness of core protected areas, we also observed a lack of integration of these areas into the wider landscape and a possible failure to ensure functional connectivity. Although the target species appear widely distributed across the core PCAs in the ecosystem, they were mostly absent from the UAs (Figure 3a–f). Because large-scale connectivity is pivotal, especially for large and wide-ranging mammals (Cisneros-Araujo et al., 2021; Riggio et al., 2022), we recommend targeted efforts in areas outside of protected areas to ensure functional
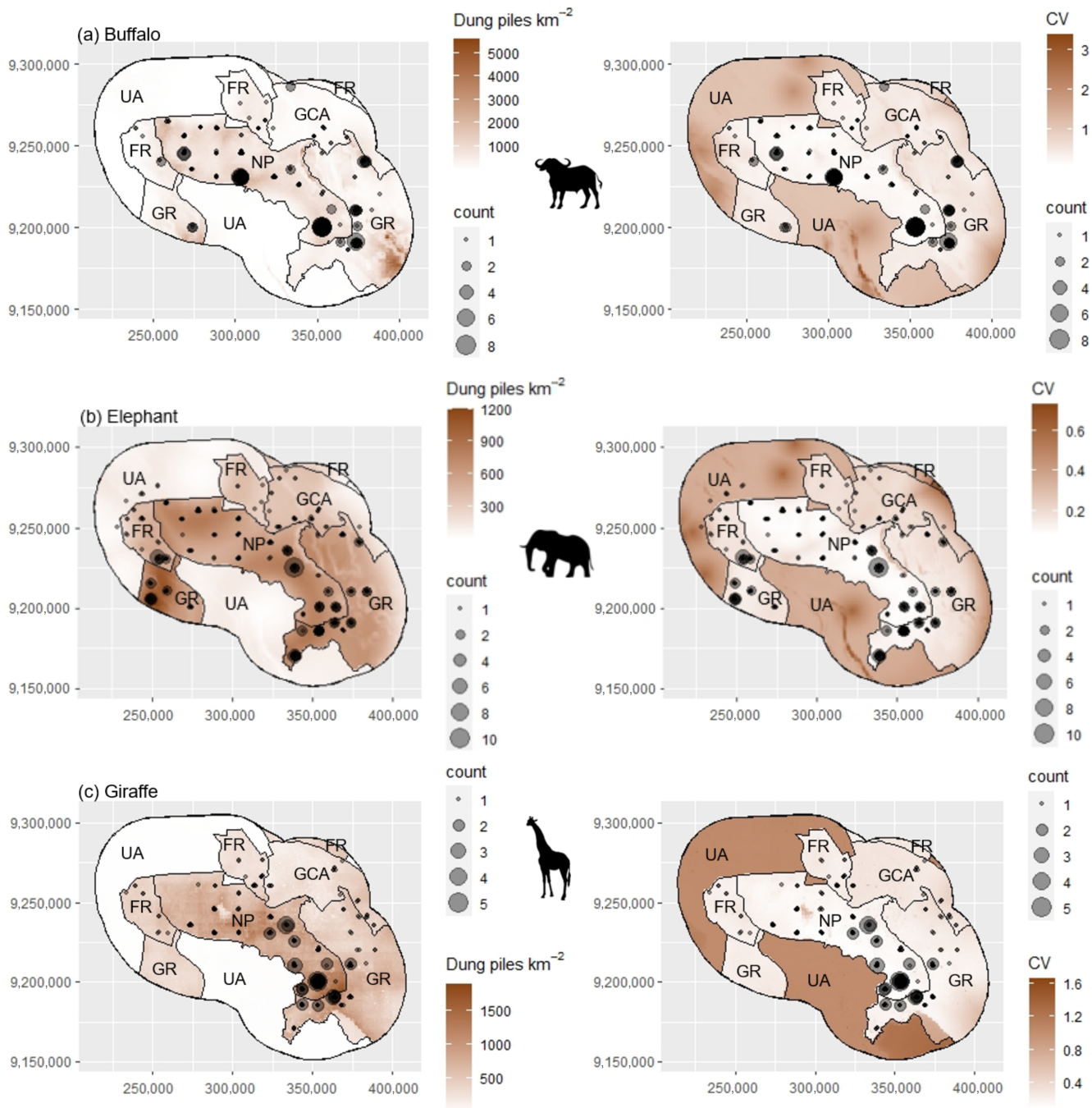
FIGURE 3 Map of dung density (dung piles per square kilometer) and associated coefficient of variation for (a) buffalo, (b) elephant, (c) giraffe, (d) hartebeest, (e) topi, and (f) zebra across protection levels (FR, forest reserve; GCA, game-controlled area; GR, game reserve; NP, national park; UA, unprotected area) of the Katavi–Rukwa Ecosystem in western Tanzania. Black and gray dots represent the distribution and magnitude of dung sighted.

connectivity to adjacent ecosystems in order to support the persistence of wildlife populations over the long term.

Similarly, our density surface models demonstrated a consistent influence of land use (especially distance to cropland) on the spatial distribution of all considered species (Table 3a–f). Generally, target species avoided areas near to cropland and partially also areas in immediate proximity to houses, suggesting that land use thrusts large mammal species further into the core areas of protected areas. Such isolation effects have also been observed in other case studies across East Africa (e.g., Msoffe et al., 2011; Newmark, 2008; Ogutu et al., 2012; Veldhuis et al., 2019), highlighting that expansion of cropland toward protected area boundaries negatively
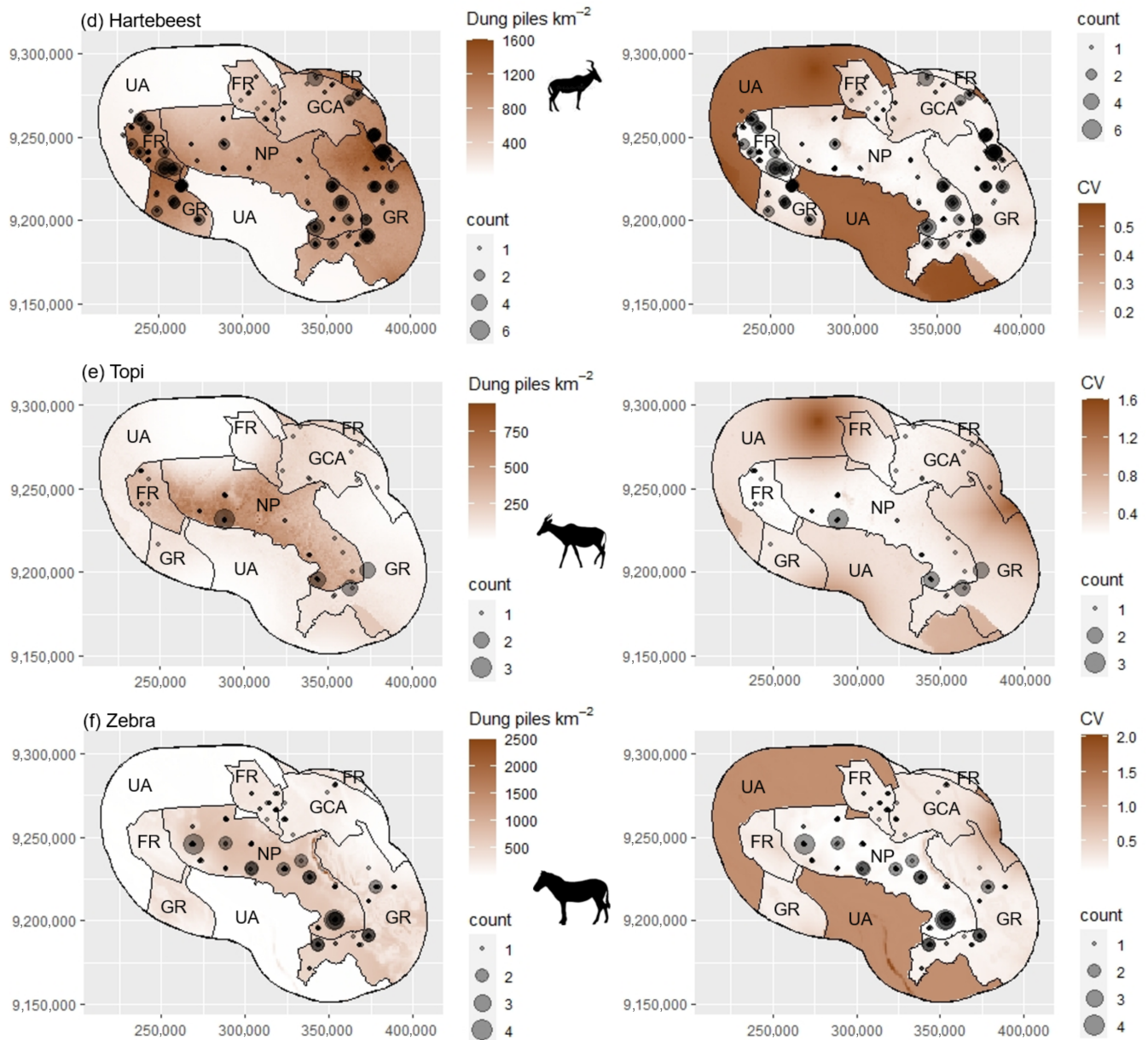
FIGURE 3　(Continued)

impairs the distribution of large mammal species while isolating the protected area further. We did not detect signs of most considered species beyond protected area boundaries (Figure 3a–f), possibly indicating the increasing unsuitability of unprotected land for wildlife to effectively serve as viable habitat. This apparent unsuitability of unprotected land has likely been increasing over the last decades due to destruction of natural habitats around protected areas of the Katavi–Rukwa Ecosystem (Giliba et al., 2022, 2023; Lobora et al., 2017) and high levels of bushmeat poaching (Martin et al., 2013). Notwithstanding, we detected high dung densities of elephant and hartebeest even in less-strictly protected areas (Figure 3b,d). Possibly, this is due to their preferences for

woodland habitats (De Knegt et al., 2011; Rodgers, 1979), which are found inside KNP to some extent but predominate in game and FR of the Katavi–Rukwa Ecosystem (Waltert et al., 2009). Notably, dung of these two species occurred at relatively high densities in areas designated for trophy hunting (i.e., GR), providing further support that hunting areas with relatively low hunting offtake can sustain substantial wildlife populations and contribute to landscape-wide conservation goals (Di Minin et al., 2016; Dickman et al., 2019).

To assess the effectiveness of our indirect survey methodology, we conducted a comparative analysis with direct wildlife surveys in the same ecosystem (Table 4). We compared our results, based on dung surveys, with

T A B L E 4 Comparison between indirect (dung density estimates, this study) and direct survey methods for estimating the densities of large herbivores in the Katavi ecosystem.

	Walking transects, dung, 2021[a]		Walking transects, sightings, 2021[b]	Aerial survey, 2018[c]
Species	**Environmental covariates considered**	**No environmental covariates**		
Buffalo				
NP	1	1	1	2
GR	2	2	2	1
GCA	4	3	Not detected	3
FR	3	4	Not detected	4
UA	Not detected	Not detected	Not detected	Not detected
Elephant				
NP	2	1	2	1
GR	1	2	1	2
GCA	3	4	Not detected	3
FR	4	3	Not detected	4
UA	5	5	Not detected	Not detected
Giraffe				
NP	1	1	1	1
GR	3	2	2	2
GCA	4	4	Not detected	Not detected
FR	2	3	Not detected	Not detected
UA	Not detected	Not detected	Not detected	Not detected
Hartebeest				
NP	2	1	1	1
GR	1	2	2	2
GCA	4	4	3	3
FR	3	3	Not detected	Not detected
UA	5	5	Not detected	Not detected
Topi				
NP	1	1	1	1
GR	4	4	Not detected	Not detected
GCA	2	3	Not detected	Not detected
FR	3	2	Not detected	Not detected
UA	Not detected	Not detected	Not detected	Not detected
Zebra				
NP	1	1	1	1
GR	2	2	2	2
GCA	4	4	Not detected	Not detected
FR	3	3	Not detected	4
UA	Not detected	Not detected	Not detected	3

Note: Estimates were compared by ranking area-specific densities within each study (1 = highest density).

Abbreviations: FR, forest reserve; GCA, game-controlled area; GR, game reserve; NP, national park; UA, unprotected area.

[a]Data from this study.

[b]Data from Kiffner et al. (2023).

[c]Data from Giliba et al. (2022).

those obtained from visual sightings of species during aerial line transects (Giliba et al., 2022) and walking transects (Kiffner et al., 2023). Findings from the dung survey indicate that most of the studied species are more widely distributed across the PCA network (Figure 3a–f) than inferred from direct survey methods. When examining the data across protection status, we observed variations in species detections across the three methods (Table 4). While all three methods detected most of the target species in NPs (all species) and GRs (all species except for topi), some species were not sighted during aerial or walking transects in GCAs (aerial survey: giraffe, topi, zebra; walking survey: all species) and FRs (aerial survey: giraffe, hartebeest, topi, zebra; walking survey: all species). Although we cannot entirely rule out the possibility of misidentifications, we consider this to have had minimal impacts on our results. It is worth noting that livestock grazing is illegal and rare in all study areas except for UA, making misidentification with livestock species (e.g., zebra–donkey, buffalo–cattle) unlikely to be a major factor. While the potential for misidentification (e.g., giraffe–eland *Taurotragus oryx*, zebra–warthog *Phacochoerus africanus*, hartebeest–topi, and hartebeest/topi–roan *Hippotragus equinus*/sable *Hippotragus niger*/waterbuck *Kobus ellipsiprymnus*) cannot completely be dismissed, we believe such instances were infrequent. Furthermore, a camera trap survey in the FR north of KNP detected all six target species (Hausser et al., 2017), providing additional evidence that these ungulates are more widely distributed than expected based on direct survey methods.

In the case of aerial surveys, we hypothesize that the discrepancy in detections is primarily due to visibility bias. With the exception of elephant and buffalo, most ungulate species are difficult to detect in woodland areas typical of our study area (Greene et al., 2017; Jachmann, 1991, 2002; Lee & Bond, 2016). In contrast, nondetection of many species along walking transects may be related to behavioral adaptations of these species. All target species are subject to illegal hunting (Martin et al., 2013), and most of them are also subject to legal hunting in GRs and GCAs. Variation in hunting pressure, which is typically greater in less-strictly protected areas in this ecosystem (Waltert et al., 2008), likely results in animals being more cautious and adjusting their flight initiation distances in response to human observers (Caro, 2005; Kiffner et al., 2014), making direct encounters in less-strictly protected areas less probable.

Additionally, the nondetection of some target species in less-strictly protected areas can be explained by availability bias. The majority of our target species are cathemeral, that is, they are active during both day and night (Clauss et al., 2021). This behavioral flexibility suggests that they might primarily use human-dominated or less-strictly protected areas during nighttime to avoid encounters with humans (de Jonge et al., 2022; Gaynor et al., 2018). Hence, the lack of sightings during aerial and walking surveys may be attributed to the species' tendency to avoid less-strictly protected areas during the day. In contrast, indirect surveys capitalize on the gradual accumulation of dung over extended time periods, thereby increasing the likelihood of detecting these species. A particular case in point is the detection of elephant dung in the northern UA (Figure 3a), providing compelling evidence that there is still, albeit limited, elephant movement outside protected areas (Giliba et al., 2023).

To determine whether differences in wildlife densities are due to environmental conditions or conservation efforts, we tested the unconditional effect of the protected area status on species-specific dung densities (Appendix S1: Table S1). Without accounting for environmental covariates, the ranking of protected area categories remained largely similar (Table 4). However, including environmental covariates influenced the density ranking for all species except zebra, suggesting that the selected environmental covariates may be more important than protection status alone. Therefore, it is important to consider environmental factors when assessing the effectiveness of conservation efforts (Rosenblatt et al., 2019).

While we cannot directly disentangle the exact causes for the observed method-related density differences, probably due to the different types of data they provide, these comparisons provide circumstantial evidence that indirect survey methods (such as dung, camera trap, or acoustic surveys) are well-suited for monitoring wildlife populations along anthropogenic gradients as they seem to be less prone to availability and visibility bias that arise from vegetation structure and behavioral adaptations of wildlife.

CONCLUSIONS

Based on our density surface models, protection level and land use impact the spatial distribution of large mammals within the Katavi–Rukwa Ecosystem. While our findings show high dung densities in strictly protected areas, our study also shows a worrying low dung density of most large wildlife species outside of these designated areas. Considering that effective and hands-off (i.e., not requiring intensive management such as translocations or supplementary feeding) conservation of wildlife populations ultimately depends on the connectivity of a network of habitats and ecosystems, a better integration of conservation efforts outside of protected areas is needed in the Katavi–Rukwa Ecosystem. The long-term survival of

mammals here and possibly also in other places on Earth can only be achieved by complementing the establishment of protected areas with effective biodiversity conservation measures across entire landscapes.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data (Giliba et al., 2024) are available from Dryad: https://doi.org/10.5061/dryad.00000007k.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.