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CONTRIBUTED PAPER

Integrating Indigenous knowledge and modern statistical approaches to model wildlife density based on animal track counts

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Abstract

In multiuse areas outside formal protection, sustaining both wildlife and people is critical to wildlife conservation and coexistence efforts. Botswana's Kalahari hosts one of sub-Saharan Africa's largest unprotected areas supporting free-ranging wildlife. The role of multiuse areas as a wildlife habitat and movement corridor is increasingly threatened by land-use change, particularly the expansion of sedentary livestock farming. In light of these changes, updated information on wildlife status and their use of these areas is lacking. Leveraging the Kalahari's sandy substrate and Indigenous tracking skills, we demonstrated the potential of animal track surveys for large-scale wildlife monitoring. We conducted biannual surveys over 3 years across 22,000 km^2 of multiuse wildlife management areas and used the Formozov–Malyshev–Pereleshin formula approach—a population density estimator—to collect large herbivore and carnivore track data. We analyzed 22,793 tracks from 13 species collected over 6222 km of transects with three objectives: estimate species population densities, identify key environmental predictors of their spatial variation, and derive predictive maps to highlight higher wildlife density areas. Although some herbivores declined, no changes in carnivore densities were detected over the study period. Cattleposts were negatively associated with most species, whereas burned areas showed contrasting associations with herbivore and carnivore densities. Vegetation characteristics and distance to mineral pans were also often associated with species density. The region still supports large wildlife and potential movement pathways—albeit less than in the past—especially away from human activity. We identified key areas for preservation in future land-use planning, with potential to also support nature-based livelihood development. Where tracking substrates and Indigenous knowledge coexist around the world, track-based monitoring can effectively inform conservation. Its cultural and economic benefits to local communities, in addition to relational engagement with the natural world, may also contribute to human–wildlife coexistence, uphold land rights, and support community-led resource management.

KEYWORDS
animal indirect signs, community-based conservation, CyberTracker, Formozov–Malyshev–Pereleshin formula, population monitoring, sdmTMB, track survey, wildlife conservation

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INTRODUCTION

The quality and availability of essential resources for all species depend on ecosystem health and balance. However, of the estimated 8 million animal and plant species living on Earth, approximately 1 million are believed to be threatened with extinction, reflecting various levels of ecosystem dysfunction (IPBES, 2019). To mitigate biodiversity loss, biological conservation primarily relies on a network of protected areas (PAs) and other effective area-based conservation measures, currently covering 17.5% of terrestrial and inland water areas (UNEP-WCMC & IUCN, 2025). This is just over half of the 30% target for 2030 set by the 15th Conference of the Parties to the Convention on Biological Diversity in late 2022. However, an additional but largely undocumented number of territories are conserved by Indigenous peoples and local communities, often through traditional stewardship (UNEP-WCMC & IUCN, 2025). Regionally, Africa slightly surpasses the global average, with 19% of its rangelands under formal protection. It also hosts the highest proportion of countries with Indigenous peoples (Garnett et al., 2018). This scenario is encouraging for further conservation efforts, as the continent harbors exceptional biodiversity, including over a quarter of the planet's mammal species (IPBES, 2018).

The semiarid Kalahari Desert (hereafter referred to as the Kalahari), spanning Botswana, Namibia, and South Africa, is a good example of an area with high biodiversity as it hosts a nearly intact megafauna assemblage. However, with scarce surface water most of the year and patchy food availability, Kalahari wildlife occurs at relatively low densities and is highly mobile, relying on connected habitats to access key resources and survive (CI, 2010; Keeping et al., 2022b; Perkins, 2019). In Botswana, the Kalahari spans two-thirds of the country (Figure 1), including its largest PAs—the Central Kalahari Game Reserve and Kgalagadi Transfrontier Park. These PAs are connected by wildlife management areas (WMAs), forming the extensive Western Kgalagadi Conservation Corridor (WKCC), which supports wildlife movement and access to resources between adjacent livestock farming areas (CI, 2010) (Figure 1). This 170,000-km^2 landscape is possibly one of the largest remaining unfenced wilderness areas in sub-Saharan Africa (WCS & CIESIN, 2005). Formally unprotected, these WMAs face anthropogenic encroachment, primarily from the expansion of livestock farming—a common land-use shift across Africa and the Global South (Hempson et al., 2017; Winkler et al., 2021). This shift creates complex challenges for wildlife conservation, rangeland sustainability, human–wildlife coexistence, and alternative socioeconomic development, all of which are further exacerbated by climate change (CI, 2010; Perkins, 2019).

Effective wildlife conservation relies on spatial and temporal data on population size, factors affecting populations, habitat use, and landscape connectivity. Systematic wildlife monitoring across large areas is therefore essential to track population trends and evaluate the efficacy of conservation interventions. Track-based survey methods have a long history in wildlife research across the globe. In particular, the Formozov–Malyshev–Pereleshin (FMP) formula was developed a century ago in Russia, where it has been extensively applied to estimate absolute animal densities from animal track (i.e., footprint) counts (Chelintsev, 1995; Formozov, 1932). In the 21st century, the approach has gained attention in English-language literature (Stephens et al., 2006) and empirical support across diverse ecosystems: in mud and clay soils in Italy (Romani et al., 2018); tropical forests in Brazil (Esbach, 2023); sandy beaches in the United States (Perkins, 2011); snow-covered landscapes in Canada (Doran-Myers et al., 2021), Bulgaria (Popova et al., 2019), and China (Gu et al., 2018); and eastern African savannas (Osipova et al., 2019). Track surveys are also cost-effective compared with more resource-intensive methods such as camera trapping or aerial surveys (Keeping, Burger, et al., 2018; Waller et al., 2024). The use of indirect animal signs has been criticized due to challenges in accounting for animal detectability, which can undermine reliability or reduce track counts to relative indices of density (i.e., indices related to the absolute density by an unknown factor) (Dröge et al., 2020; Hayward et al., 2015; Karanth et al., 2003). The FMP formula addresses these challenges by inherently accounting for animal detectability along transects and, when needed, allowing correction for the probability of track detection by observers (Gielen et al., 2024). Importantly, as a random encounter model, it does not require individual track recognition.

Similar to species in other ecosystems worldwide, larger vertebrate species in the Kalahari are a key focus due to their space requirements, umbrella effect, tourism value, and vulnerability to disturbance (Lindsey, Alexander, et al., 2007; Malhi et al., 2016; Ripple et al., 2014, 2015). The region's sandy terrain and the presence of traditional Indigenous peoples with tracking skills make it an ideal area to study animals through their tracks. The FMP formula has been used in the region since 2008 and has shown promising results for estimating absolute wildlife densities (Ahlswede et al., 2019; Gielen et al., 2024; Keeping, Burger, et al., 2018). Recently, FMP-based track surveys conducted between 2008 and 2018 enabled comprehensive modeling of wildlife occupancy and landscape connectivity across the WKCC (Keeping et al., 2022a, 2022b), providing the foundation for its Integrated Land Use Management Plan (ILUMP) (Tshukudu, 2025a, 2025b), which is awaiting implementation. At the same time, anthropogenic development continues to expand, highlighting the need for follow-up research. A participatory approach inclusive of local community members can generate mutual benefits, potentially improving socioeconomic conditions, promoting human–wildlife coexistence, and enhancing conservation outcomes (Dickman et al., 2025; Jolly & Stronza, 2025; Lilleyman et al., 2022).

Harnessing the region's assets, we demonstrated the potential of track surveys for large-scale wildlife monitoring and conservation through multiple outputs derived from a single-track dataset. Using the northern part of the WKCC as a case study, we partnered with Indigenous trackers to conduct biannual track surveys from 2019 to 2021. Track data, collected using the FMP formula approach, were analyzed to

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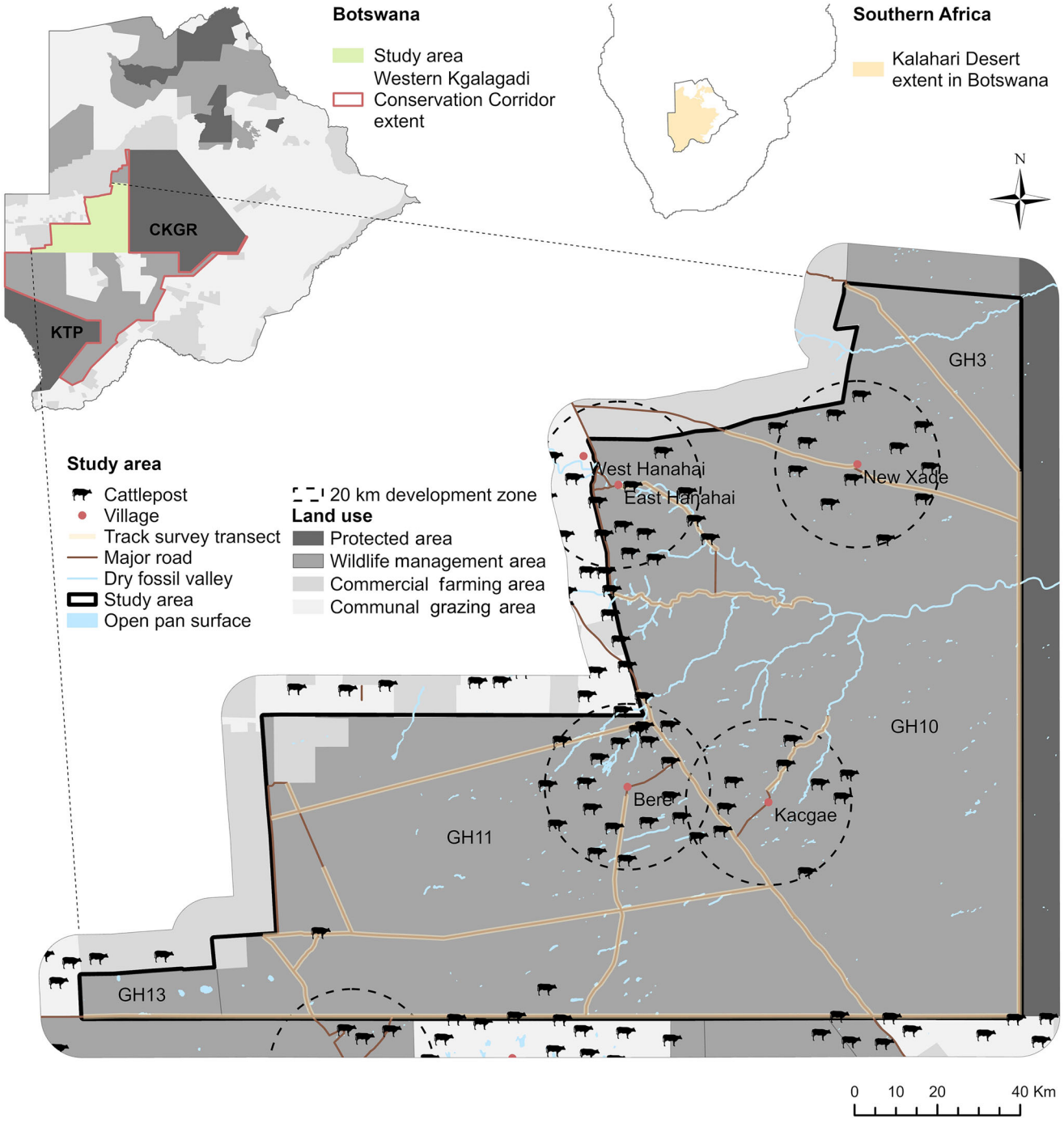


FIGURE 1 Location of the study area and its landscape features within the Western Kgalagadi Conservation Corridor (WKCC). Together with the Central Kalahari Game Reserve (CKGR) and Kgalagadi Transfrontier Park (KTP), the WKCC forms an extensive unfenced wilderness—one of the largest in sub-Saharan Africa—supporting free-ranging wildlife within the Kalahari Desert of Botswana.

address our three main objectives: estimate absolute population densities of 12 large and one medium wildlife species (hereafter collectively referred to as large), identify key predictors of species' relative density (using relative track densities as proxies), and derive predictive maps across the entire study area to highlight areas with higher relative density of wildlife. From a management perspective, our results already have informed and will continue to support conservation decisions and land-use planning to protect and sustainably develop this region. In parallel, by demonstrating the versatile use of track data, we sought to promote research methodologies that involve collaboration with local communities, both in the Kalahari and in other regions worldwide with suitable tracking substrates.

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MATERIALS AND METHODS

Study area

Botswana land use is primarily divided among partly unfenced PAs, unfenced WMAs, fenced commercial farming areas with enclosed farms, and unfenced communal grazing areas that include cattleposts, arable land, and residential zones. WMAs are designated for the sustainable use of natural resources, acting as buffer zones for PAs or serving as ecological corridors for wildlife movement (Government of Botswana, 1986; Parry & Campbell, 1990). Together, PAs and WMAs support most of Botswana's viable populations of large wildlife species (DWNP, 2015, 2018).

We surveyed four WMAs in the Ghanzi District, Botswana: GH10, GH11, GH13, and the southern part of GH3 (Figure 1). Together, they span approximately 22,000 km^2 on a plateau between 21.7°–23.3°S and 20.6°–22.8°E, forming the northern section of the WKCC (Figure 1). The sandy ground supports grasses, shrubs, and scattered trees, forming a generally open savanna depending on local climatic and soil variations (Skarpe, 1986; Weare & Yalala, 1971). Annual rainfall averages 400 mm, falling almost exclusively during the rainy season from November to April (Batisani & Yarnal, 2010; DMS, 2021). Natural surface water is ephemeral, found only in isolated clay depressions called pans or parts of fossil valleys after rainfall (Lancaster, 1974). The study area also includes four villages, each with a 20-km development zone for exclusive use (Ministry of Local Government, 2009) (Figure 1). Within these zones and adjacent communal grazing areas, cattleposts—free-ranging livestock systems centered around water points supplied by underground water (Perkins, 1996)—have been prioritized over wildlife-based livelihoods. We recorded 97 cattleposts (during the study period) within the development zones, plus a 10-km communal grazing area buffer around the study area's perimeter. In the absence of fences, livestock regularly encroach on WMAs (Van der Weyde, 2019). Livestock from fenced farms (commercial farming areas) bordering some WMAs occasionally graze within them due to poor fence maintenance. Roads are sparse, mostly sand tracks with low traffic, except for a single tarred road marking the boundary between GH10 and GH11.

Species density, distribution, and movements are shaped by a combination of ecological and anthropogenic variables. Ecological variables such as rainfall are seasonal and often localized in the Kalahari, dramatically affecting vegetation productivity on which large herbivores depend (van Rooyen & van Rooyen, 1998). In turn, large carnivores rely on prey availability (Mills, 1984). Species may favor denser or more open vegetation cover depending on their foraging strategies or antipredator adaptations (Bothma & Walker, 1999; Smithers, 1971). Pans and dry fossil valleys provide seasonal water, as well as nutrient-rich vegetation and mineral licks, particularly valuable for grazers, especially during the calving season (CI, 2010; Parris & Child, 1973). Anthropogenic variables primarily relate to settlements and livestock farming. Cattleposts, and to a lesser extent fenced farms, are focal points for human–wildlife conflict (Karunya Consulting et al., 2020; Klein, 2013). They often drive wildlife habitat loss and land degradation within WMAs (Cooke, 1985; Parris & Child, 1973; Verlinden et al., 1998) and may serve as precursors to poaching activities (Senyatso, 2011; Thouless, 1998). Fenced farms bordering some WMAs can also restrict the movement of some large wildlife species (Van der Weyde et al., 2021). Finally, wildfires, mostly human-induced, occur annually in the dry season. They trigger green vegetation flushes with the first rains of the wet season (Maabong & Mphale, 2021; Skarpe, 1980), usually attractive to herbivores (Ngwamotsoko, 1985; Verlinden, 1997).

Species data collection

We conducted track surveys biannually during 2019–2021, in May (June in 2020 due to COVID restrictions) and November, to collect track data on 13 large species: eland (*Taurotragus oryx*), gemsbok (*Oryx gazella*), red hartebeest (*Alcelaphus buselaphus caama*), greater kudu (*Tragelaphus strepsiceros*), blue wildebeest (*Connochaetes taurinus*), ostrich (*Struthio camelus*), springbok (*Antidorcas marsupialis*), African wild dog (*Lycaon pictus*), brown hyena (*Hyaena brunnea*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), lion (*Panthera leo*), and spotted hyena (*Crocuta crocuta*). May and November mark the transition between the dry and wet seasons; thus, carrying out our study during this time avoided the peak rainy period potentially challenging for track collection. November signifies the onset of the first rains, usually prompting wildlife, particularly large herbivores, to move toward areas where storms occur. In May, they begin to select areas that locally received higher rainfall in previous months, likely to maintain quality vegetation longer and support water-laden melon and cucurbit crops (Bonifica, 1992; Ngwamotsoko, 1985; Verlinden & Masogo, 1997; Williamson et al., 1988). Therefore, these months are particularly useful for detecting wildlife moving through the landscape.

Each survey sampled the same 1037 km of transects, starting from the northeast of the study area (GH3–GH10) and ending in its western part (GH11–GH13) (Figure 1). Transects covered almost all existing low-traffic roads in the study area, including 783 km of sand roads and 156 km of sand-covered gravel roads, with an additional 98 km surveyed off-road along the western side of the tar road marking the GH10–GH11 boundary. Transects sampled gradients of environmental predictors representative of the study area's environmental variation (Appendix S1) and intercepted historical wildlife movement routes. The data collection team consisted of a single vehicle driven by a recorder and a pair of Indigenous certified trackers sat in front of the vehicle as observers (see Appendix S2 for details on survey personnel). Driving speed was capped at 10 km/h but was reduced when track visibility decreased. Upon detection, animal track interceptions with the transect were logged on a CyberTracker (https://cybertracker.org/) application on a smartphone, recording date, time, species, number of individuals, track age class (i.e., ≤24 h, 2 days, >3 days, ≥1 week, and ≥1 month), and GPS location (Appendix S3). Under the FMP model, one track interception represented the intersection between one individual animal's movement path and the survey

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transect, visible as one or a series of footprints on the transect. Each track interception was counted irrespective of individual identity and the number of footprints. When an animal was clearly traveling on the transect (e.g., some carnivores), it was counted only once to preserve the assumption of independence between movement paths and transects (see Gielen et al. [2024] for additional details on sampling protocol).

Absolute population density estimates

The FMP formula estimates the absolute population density ($\hat{D}$) for the study area by scaling the estimated number of fresh (≤24-h old) track interceptions ($\hat{x}$) counted along the total transect length S (i.e., track index $\frac{\hat{x}}{S}$) by the estimated average distance the species travels in 24 h ($\hat{M}$) within the study area. The term $\frac{\pi}{2}$ accounts for the effect of animal movement path direction, averaging over all angles at which the path may cross the transect (Kondratenkov, 2019; Stephens et al., 2006):

$$\hat{D} = \frac{\pi}{2} \cdot \frac{\hat{x}}{S \cdot \widehat{M}}. \quad (1)$$

The probability that an animal movement path intersects with the total transect length at least once ($\widehat{p_1}$) is inherently accounted for by all the FMP parameters, of which the accuracy of $\hat{M}$ is key (see Additional File 1 in Gielen et al. [2025]). The probability of fresh track detection by observers ($\widehat{p_2}$) in the study area was estimated at 0.75 for large antelopes and 0.86 for large carnivores (excluding brown hyena) and ostrich, based on data from Gielen et al. (2024). These values were used to correct the observed number of fresh track interceptions (x), such as $\hat{x} = \frac{x}{\widehat{p_2}}$. For brown hyena, $\widehat{p_2}$ was estimated at 1 due to the species' high propensity to follow linear landscape features for extended distances (Mills, 1990), making them hard to miss on our transects (personal observation).

For each of the 13 species, the absolute density estimate was calculated for both the entire study area and its two main regions (GH3–GH10 and GH11–GH13) by directly inputting parameter values into the formula. Empirical $\hat{M}$ values collected in the Kalahari region were used for all species except springbok, for which data were insufficient to capture the species' full movement range (see values in table 1 of Gielen et al. [2025]). For this species, an allometric estimate based on the body mass–daily travel distance relationship in artiodactyls was used (Carbone et al., 2005) and further corrected with a Kalahari coefficient of 1.917 (Gielen et al., 2025). We used the same species-specific $\hat{M}$ across seasons due to limited data availability and limited seasonal variation suggested for some of the large herbivore species (Gielen et al., 2025). The uncertainty around $\hat{D}$ was calculated as bias-corrected and accelerated 95% confidence intervals via nonparametric bootstrapping (Keeping, 2014). To obtain population abundance, $\hat{D}$ was multiplied by the total size of the study area or region (in km^2). All analyses, including those described below, were conducted in R (version 4.4.1).

Relationships between relative track density and environmental predictors

To estimate relative track density, we first rasterized the study area into 4-km^2 grid cells, then assigned each track interception data point to a cell. The cell's width corresponded to approximately half the $\hat{M}$ of springbok and a surface area approximating half its home range ($\sim\hat{M}^2$ according to Stephens et al. [2019]). As springbok was the least mobile of our study species, this choice represented a good compromise between having enough grid cells with track detection and a fine enough resolution to produce spatial outputs that could inform land-use planning.

In our low-density environment, the number of fresh (≤24-h old) track interceptions was limited, potentially yielding a null $\hat{D}$ for a large proportion of grid cells, especially for rare species. We included older tracks (i.e., tracks under a week old) to utilize most of the collected data, increasing the number of grid cells with tracks present. When retaining older tracks in $\hat{x}$, the track index ($\frac{\hat{x}}{S}$) was used on its own as an estimate of relative track density for each grid cell, serving as a proxy for relative animal density in place of the absolute density $\hat{D}$. This approach was valid at the species level, as $\hat{M}$ and $\widehat{p_2}$ were assumed sufficiently constant across the study area and time period (Gielen et al., 2025, 2024). Therefore, within each grid cell and for each of the six surveys, a species-specific relative track density was calculated as the number of individual track interceptions (under a week old) per transect length contained in the grid cell (this methodological choice is further justified in Appendix S2).

We extracted the values of the environmental predictors in each grid cell for each survey (Table 1). A relative prey density map for carnivore models was created by summing herbivore predicted relative track density layers, with each weighted by the inverse of the species' estimated daily travel distance. All continuous predictors were standardized using z-scores within each survey (general information on the creation of predictor layers is provided in Appendix S2; Appendix S4 outlines steps for layer creation in ArcMap 10.8; and Appendices S5 & S6 provide Google Earth Engine code for extracting vegetation data).

For each species, we modeled relative track density as a function of the fixed-effect environmental predictors using spatial geostatistical generalized linear mixed models via the sdmTMB package (Anderson et al., 2024; the strategy followed several steps illustrated in Appendix S2). Spatially correlated random effects were incorporated through a triangulated mesh of vertices, approximating spatial variability in observations based on the latitude and longitude centroids of each grid cell (projected in EPSG:102022, WGS 1984 datum). Survey identity was included as a random intercept.

We used the Akaike information criterion (AIC) to identify the best distribution family for the response variable. For herbivores and two carnivores (lion and African wild dog) with high data dispersion, AIC supported the use of hurdle models with two components: one for zero versus nonzero outcomes and another for positive values. For the other four carnivores with lower data dispersion, we applied a Tweedie distribution. We followed the same approach to identify the appropriate struc-

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TABLE 1 Response variable and environmental predictors used to model track density.

Variable type	Model component	Variable name (name in model)	Description	Range of value per grid cell	Expected relationship to response variable	Source
Response—continuous (survey specific)	Response	Relative track density (Species name, e.g., Gemsbok)	Estimated number of individual track interceptions (≤24 h to 6 days old) per kilometer of transect	0–82 km^{-1} (across all species and surveys)	NA	Six biannual track surveys (2019–2021) conducted along 1037 km of transects in GH3/10/11/13 WMAs, Ghanzi District, Botswana
Predictor—continuous (survey specific)	Main fixed effect	Distance to cattlepost (Dist_Cattl)	Distance to the closest cattlepost at the time of the survey	0–56 km (across all surveys)	Positive relationship	Remote sensing ground-truthed by field visits between 2019 and 2021
Predictor—continuous (survey specific)	Main fixed effect	Distance to commercial farming area (Dist_CFA)	Distance to the closest fence of the closest fenced farm at the time of the survey	0–85 km (across all surveys)	Positive relationship	National land-use map obtained from Ngami Data Services in 2009 supplemented by remote sensing
Predictor—continuous	Main fixed effect	Distance to pan (Dist_Pan)	Distance to the closest edge of the closest pan	0–30 km	Negative relationship for herbivores, maybe indirectly for carnivores too	Remote sensing done by Arthur Albertson Consulting in 2024 and this study
Predictor—continuous	Main fixed effect	Distance to major pan (Dist_Pan50)	Distance to the closest edge of the closest pan of minimum 500 m^2	0–44 km	Negative relationship for herbivores, maybe indirectly for carnivores too	Remote sensing by Arthur Albertson Consulting (2024) and this study
Predictor—continuous	Main fixed effect	Distance to fossil valley (Dist_Valle)	Distance to the closest fossil valley line feature	0–98 km	Idem as above	Remote sensing by Arthur Albertson Consulting (2024) and this study
Predictor—continuous	Main fixed effect	% Grass (Grass_cove for herbivores and Grass_co_c for carnivores)	Proportion of 10-m grass pixels within a zone of 3 × 3 grid cells (the grid cell of interest and its eight neighboring cells) for herbivores, and a zone of 5 × 5 grid cells for carnivores	0–87% and 0–64%	Relationship depending on the species	Maximum likelihood supervised classification on Sentinel-2 10 m imagery median values from November 2019 and June 2020
Predictor—continuous	Main fixed effect	% Shrub (Shrub_cove and Shrub_co_c)	Idem as above, for shrub (~<2–3 m)	0–90% and 0–84%	Idem as above	Idem as above
Predictor—continuous	Main fixed effect	% Large tree and shrub (Tree_cover and Tree_cov_c)	Idem as above, for large tree and shrub (~>2–3 m)	0–55% and 0–37%	Idem as above	Idem as above
Predictor—continuous (survey specific)	Main fixed effect	Burned area (Burned)	Binary variable indicating whether a grid cell burned (1) or not (0) during the previous dry season (May–October), used for each November survey and the subsequent May/June survey (i.e., lagged fire variable)	0, 1	Positive relationship as burned ground produces high-quality vegetation during regrowth	MODIS MCD64A1 Burned Area Product 500 m

(Continues)

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TABLE 1 (Continued)

Variable type	Model component	Variable name (name in model)	Description	Range of value per grid cell	Expected relationship to response variable	Source
Predictor—continuous (survey specific)	Main fixed effect	Modified soil-adjusted vegetation index (MSAVI)	Index of vegetation density and health	−0.06 to 0.68 (across all surveys)	Positive relationship	MSAVI equation applied to Sentinel-2 10 m imagery median values for each survey period
Predictor—continuous (for large carnivores only)	Main fixed effect	Relative track density of prey species (Prey_densi)	Weighted sum of large herbivore track densities predicted through this study at the time of the survey	0–4 km^{-1}	Positive relationship for species focusing on large prey	Six biannual track surveys (2019–2021) conducted along 1037 km of transects in GH3/10/11/13 WMAs, Ghanzi District, Botswana
Predictor—continuous (survey specific)	Main fixed effect	Cumulative rainfall (Cum_rainfa)	Cumulative rainfall over the previous wet season for November surveys, and from October 1 to the day before the grid cell was surveyed for May/June surveys	160–795 mm (May/June) and 0–82 mm (November)	Positive relationshngip	TAMSAT 4 km imagery (Maidment et al., 2014, 2017; Tarnavsky et al., 2014)
Predictor—categorical	Main fixed effect	Region (Region)	Region separation of the study area at the level of the tar road marking the GH10–GH11 boundary, potentially affecting wildlife distribution, to account for possible spatial effects	GH3–GH10, GH11–GH13	Relationship depending on the species	National land-use map from Ngami Data Services (2009)
Predictor—continuous	Spatial random effect	Latitude (Y)	Latitude of the grid cell centroid to account for spatial autocorrelation	−21.732863 to −23.322910		ArcMap 10.8. (ArcGIS Desktop)
Predictor—continuous	Spatial random effect	Longitude (X)	Longitude of the grid cell centroid to account for spatial autocorrelation	20.588280–22.798370		ArcMap 10.8. (ArcGIS Desktop)
Predictor—categorical	Random intercept	Survey (Survey)	To account for the fact that each survey might have a different starting level of relative track density due to unobserved factors	May 2019, November 2019, June 2020, November 2020, May 2021, November 2021		Six biannual track surveys (2019–2021) conducted along 1037 km of transects in GH3/10/11/13 WMAs, Ghanzi District, Botswana

Note: For temporally dynamic variables, labeled as survey specific in the Variable type column, a spatial layer was created for each survey.

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ture for fixed-effects terms and the optimal spatial mesh size, ultimately creating a full model that included all fixed-effect predictors. If two predictors were highly correlated (Pearson correlation coefficient >0.7), then the one that most improved the AIC of the full model (when excluding these predictors) was retained. From the full model, we derived a small subset of ecologically meaningful models. We compared the subset models with the full model and used AIC to identify the best-fitting model to observed data. The coefficients of the predictors retained in the best selected model were examined to assess their associations with relative track density. If multiple models had a ΔAIC ≤1 compared with the best-fitting model, then the model with the most predictors was selected for this assessment. If the number of predictors was equal, then the model with the lowest AIC was retained; we prioritized preventing false negatives (i.e., missing important predictors) over false positives, given the potential ecological and management costs of overlooking important drivers. Model diagnostics were conducted by visually inspecting randomized quantile residuals (see Appendices S7–S18 for data samples and R scripts for gemsbok, brown hyena, and springbok as examples detailing sdmTMB model building and model comparison).

Prediction of relative wildlife density

For each species, we assessed the predictive performance of the full and subset models created in the previous section through *k*-fold cross-validation (via sdmTMB_cv[]). Folds were defined by spatial *k*-means clustering of grid cell centroid locations to account for spatial dependence (Anderson et al., 2026). The models' relative predictive performance was evaluated using the total log-likelihood summed across folds. Model fit was assessed using the area under the receiver operating characteristic curve (AUC) for the binomial component of hurdle models (AUC ≥ 0.7 was considered acceptable). For the Tweedie models or the positive component of the hurdle models, we used the mean absolute error (MAE). Then, for each species, we combined the predictions from models with a stacking weight >0 (Yuling et al., 2018) to generate a single, integrated map of predicted relative track density (see Appendix S2 for methodological details and Appendices S7–S18 for R scripts detailing model cross-validation and prediction).

As described previously, species relative track density maps served as proxies for species relative density. We then generated two composite maps—carnivore and herbivore relative density—by summing species-level predictions weighted by the inverse of their respective $\hat{M}$ (as in the FMP equation). This approach ensured that species' relative densities were respected. Finally, to highlight areas of higher wildlife density across the landscape, two additional maps were created that showed carnivore and herbivore relative density values above the 20th and 40th percentiles, respectively. These percentile values were chosen based on the quasinormal distribution of carnivore and Pareto-like distribution of herbivore relative density data. Separating analyses by guild enabled an investigation of specific responses to anthropogenic disturbance and potential links to adjacent areas of the WKCC, providing insights into possible drivers of human–carnivore conflict.

RESULTS

We collected a total of 25,357 tracks across 14,450 locations for all 13 species combined. Of these, 9577 fresh tracks were used for absolute population density estimations, whereas 22,793 tracks up to 6 days old were included in the spatial analyses that used relative track density estimates. The spatial grid comprised 7765 cells of 4 km^2. On average, 597 cells were sampled per survey, resulting in a total of 3852 data points for each species' spatial analysis.

Absolute population density estimates

Gemsbok was the most abundant species across the study area, followed by red hartebeest, greater kudu, and ostrich (Figure 2). Herbivores accounted for 97% of the total species abundance compared with 3% for large carnivores. Species abundance differed between regions, with blue wildebeest, springbok, and spotted hyena primarily recorded in GH11–GH13 and lion exclusively recorded in GH3–GH10.

No significant changes in large carnivore density were detected over the 3-year study period. All herbivore species tended to decline, with significant decreases in blue wildebeest and springbok ($\beta_1 = -0.89$ and -0.57, respectively, $p \leq 0.05$) and marginally significant declines in red hartebeest and greater kudu ($\beta_1 = -2.25$ and -7.4 0, respectively, $p \leq 0.10$) (Figure 3). Survey- and region-specific density estimates and their half relative confidence interval widths for all species were also determined (Appendix S19).

Relationships between relative track density and environmental predictors

Overall, relative track density was associated with all environmental predictors to varying degrees depending on the species (Figure 4). Track density was negatively associated with cattleposts for all species, except springbok, African wild dog, and, to a lesser extent, cheetah. This pattern was prominent for gemsbok, eland, and lion, which are known for their sensitivity to human disturbance. Herbivore track density was positively associated with burned areas, whereas the opposite was generally true for carnivores. For most species, track density was associated with vegetation characteristics more than the rainfall they depend on, although the magnitude and direction of this association varied among species. The distribution of mineral pans and fossil valleys was generally positively associated with herbivore track density, while showing mixed relationships for carnivores. Finally, regional differences also emerged, consistent with patterns described in the previous section (see Appendix S19 for species-specific results and interpretation).

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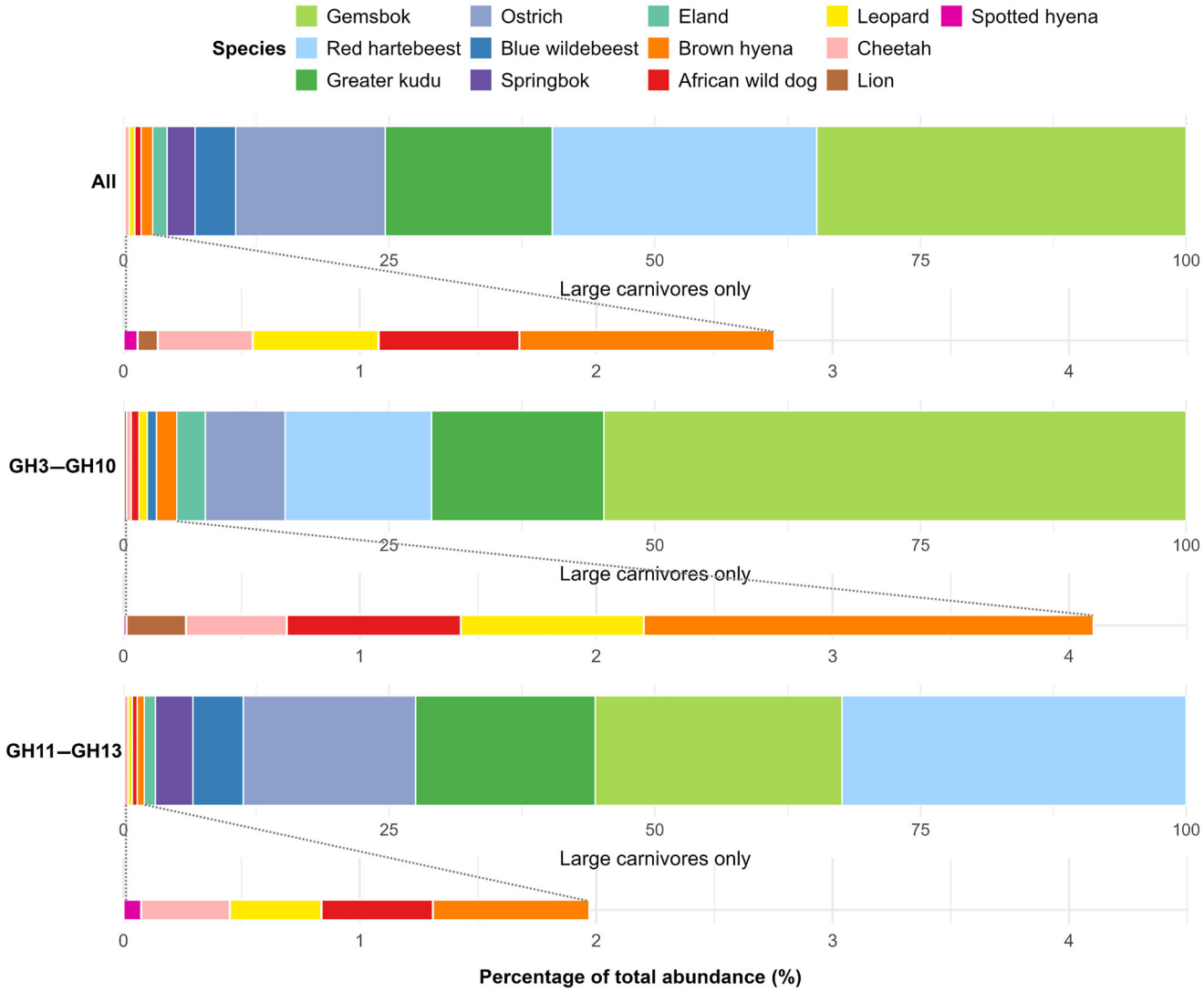


FIGURE 2 Percentages of total abundance for the 13 species studied, displayed in ascending order of percentage and organized by region (all represents the entire study area; GH3–GH10 represents the eastern region; and GH11–GH13 represents the western region). For each region, a zoomed-in view of the carnivore species is shown below the main bar plot.

Prediction of relative wildlife density

For most species, multiple subset models—and in rare cases, the full model—returned similar predictive performances, thus contributing simultaneously to relative track density predictions based on their stacking weights. The binomial components of the hurdle models (i.e., presence vs. absence of tracks) performed well, with AUC values ranging from 0.66 to 0.92. For the positive components of hurdle and Tweedie models (i.e., track density), predicted relative track density values showed a central tendency close to the mean observed values for all species, but they generally underpredicted the higher observed values. This finding was unsurprising for ecological data with high dispersion because models focused on the smaller values that dominate the dataset. Although absolute predicted values were therefore not reliable (nor was that the goal), relative increases in observed values were matched by relative increases in predicted values within the central data range (see Appendix S19 for species-specific model performance results).

Predicted relative track density maps were generated for the 13 species across the study area (Figure 5). For herbivores—and to a lesser extent, for carnivores—higher relative density was primarily found away from cattlepost areas (Figure 6). The pan-rich habitat in the southern and western parts of GH11–GH13 appeared to support the greatest species diversity. The highest densities were concentrated in the same area and along the Central Kalahari Game Reserve boundary. The two ecological corridors identified by CI (2010) between the study area and adjacent WMAs in the south (KD1 and KD5–KD6) appeared to still be used by wildlife, particularly Corridor 1 (to KD1), which is the largest. However, species-specific differences existed: brown hyena, gemsbok, and possibly eland showed greater relative density within Corridor 2 (to KD5–KD6). Animal crossings between GH11–GH13 and GH3–GH10 were mostly limited to a narrow swath in the least disturbed zone

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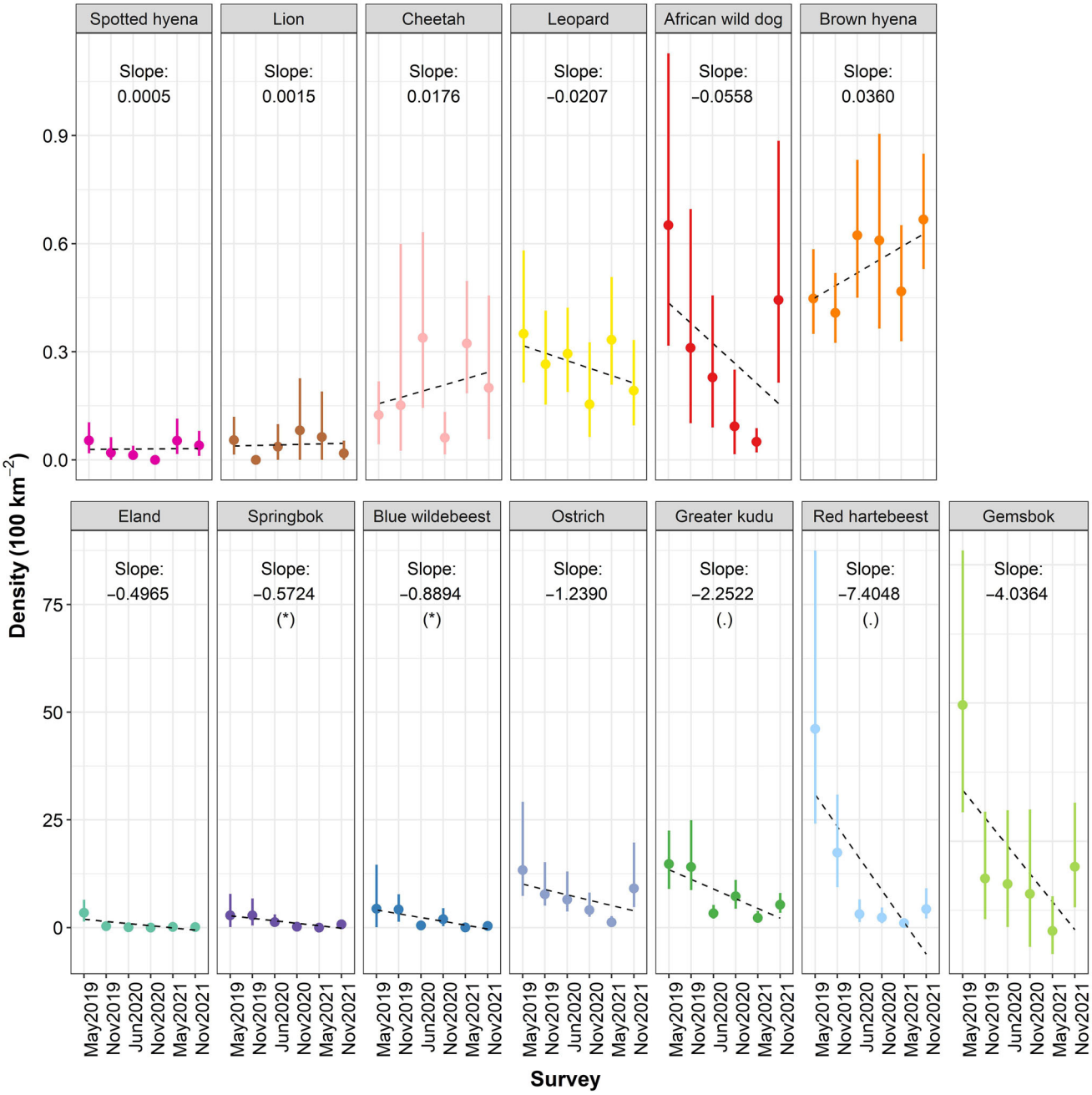


FIGURE 3 Absolute population density estimates per survey per species for the entire study area. Species-specific linear regression lines across surveys are shown as dashed lines, with slope coefficients provided. A (.) or (*) next to a slope indicates marginal significance ($p \leq 0.10$) or significance ($p \leq 0.05$) in its deviation from zero, respectively. Survey months indicated beneath the bottom *x*-axis are applicable to the top *x*-axis as well.

across the tar road, south of Kacgae village's last cattleposts (Figure 5). This potential movement pathway was more evident for herbivores, but carnivores may also use a potential link through GH9, connecting the Okwa Valley in GH10 to GH11's northern boundary (Figure 6b,d).

DISCUSSION

Building on the strong theoretical foundation of the FMP formula, we demonstrated the versatile use of track data, derived from a single dataset. Our analysis differs from the more traditional use of animal track data in a presence–absence framework (Southgate et al., 2007; Thorn et al., 2011; Van der Weyde et al., 2022) and generated complementary findings.

Track surveys for wildlife population monitoring

By surveying nearly all accessible low-traffic roads in our study area, our sample penetration was approximately 0.5 km per 10 km^2. This coverage was probably reasonable for species with

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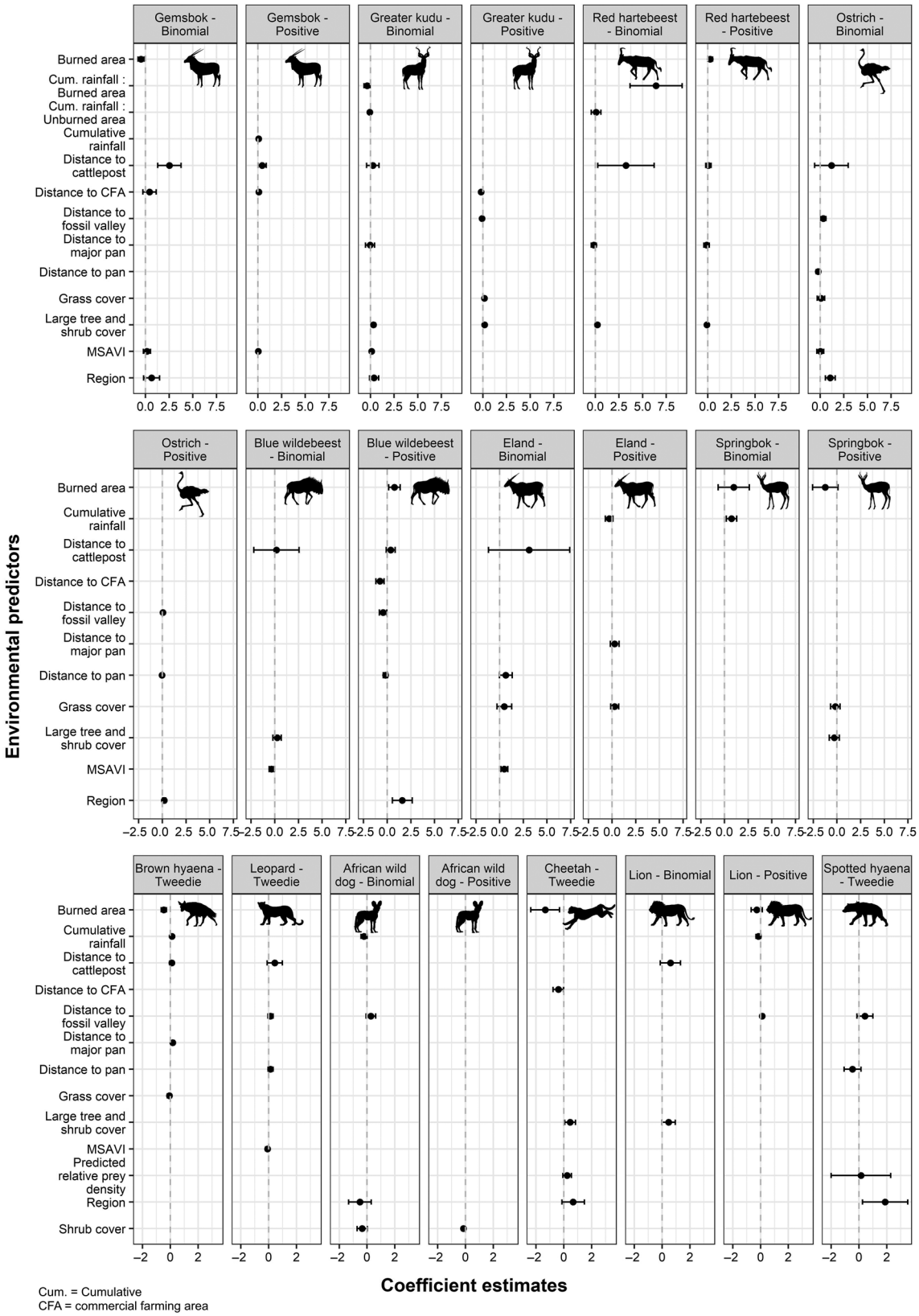


FIGURE 4 Coefficient estimates (log scale for positive and Tweedie models; log-odds scale for binomial models) with 95% CI for predictors retained in each species' best-fitting relative track density model. Grass and shrub cover (%)—strongly negatively correlated ($r = -0.86$ for herbivores, $r = -0.87$ for carnivores)—were never included together in a model; a positive effect of grass cover implies a negative effect of shrub cover, and vice versa. The modified soil-adjusted vegetation index (MSAVI) indicates green vegetation, which can reflect both vegetation health and total cover (Chen & Gillieson, 2009; Purevdorj et al., 1998; Qi et al., 1994). Icon sources: African wild dog, brown hyena, cheetah, leopard, and spotted hyena from PhyloPic (CC0 1.0). Greater kudu from PxHere Team (CC0 1.0). Springbok and eland by Robert Hering, gemsbok by T. Michael Keesey, and red hartebeest by Jan A. Venter, Herbert H. T. Prins, David A. Balfour, and

(Continues)

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FIGURE 4 (Continued)

Rob Slotow (vectorized by T. Michael Keesey) from PhyloPic (CC BY 3.0). Lion by Gabriela Palomo-Munoz and blue wildebeest by Graham Montgomery from PhyloPic (CC BY 4.0).

large daily travel distances. However, additional survey effort, particularly in the core of GH10, may improve absolute density estimate precision (Keeping & Pelletier, 2014; Stephens et al., 2006) and enhance the ability to assess trends over time. Notably, confidence intervals around density estimates will inherently have a certain width due to the uncertainty of $\hat{M}$, which can vary depending on the data used, and the variability in $\frac{\hat{x}}{\hat{s}}$ across transects, which is influenced by animal movement path tortuosity, variability in group size, and variability in true local animal density. Variability in $\frac{\hat{x}}{\hat{s}}$ can be mitigated by adjusting transect design or applying poststratification. Additionally, $\hat{M}$ would then require ongoing refinement, as it has a direct inversely proportional effect on the accuracy of density estimates. Further research should better investigate temporal variation in species-specific $\hat{M}$, such as between seasons. Additional off-road transects, where feasible, may improve transect independence from animal movements (an FMP assumption), particularly for large carnivores that often use roads (Abrahms et al., 2016; Hägerling & Ebersole, 2017). However, D. Keeping (personal communication 2025) found no significant difference in $\hat{D}$ between road and off-road transects in the neighboring Kgalagadi WMAs, suggesting animals use roads opportunistically rather than actively seeking them, except for brown hyenas. Thus, this species' density may have been overestimated, a bias that could be addressed by adjusting transect design or calibrating with alternative methods (e.g., camera trapping).

Regarding overall trends, the Kalahari experiences regular droughts (Tyson, 1980), often causing temporary wildlife declines, to which Kalahari wildlife is usually resilient. However, in past decades, increasing anthropogenic development has directly affected wildlife populations and also diminished their ability to recover from drought (Child, 1972; Perkins, 2019). Consequently, several ungulate populations, including blue wildebeest, red hartebeest, and springbok, have experienced declines exceeding 80% over the past half-century (from aerial surveys in DHV [1980], Bonifica [1992], Thouless [1998], DG Ecological Consulting [2010], and DWNP [2015, 2018]). Although short-term trends (e.g., 3 years) should be interpreted with caution in such a dynamic ecosystem, the decline in some large herbivores in our study area warrants close monitoring. Over the study period, contributing factors likely included the 2018–2019 drought, which was supported by the discovery of numerous red hartebeest carcasses near transects during the November 2019 survey. Additionally, the substantial addition of new cattleposts between 2015 and 2021 around WMA villages may have further displaced wildlife into the core areas of WMAs and PAs. The 2020–2021 wet season had above-average rainfall, potentially contributing to the slight recovery observed in some species by November 2021.

Botswana reopened trophy hunting in 2019, which has been in effect in 2020, to provide a key income source for remote communities living alongside wildlife. In the four WMAs within our study area, 16 leopards were allocated for the 2025 trophy hunting season (Government of Botswana, 2024). This amount represents 25% (95% CI: 20–32%) of the estimated local population of 63 individuals (95% CI: 50–81), including the unsurveyed northern portion of GH3. This quota therefore exceeds the typically sustainable offtake rate of 2–5% of the male population (Bond et al. [2004] in Lindsey, Frank, et al. [2007]). A quota review at the district level is urgently needed, but a shift to age-based quotas (e.g., ≥7 years old) is preferable for population sustainability (Packer et al., 2009). Leopards also undergo retaliatory removals in the context of livestock predation conflicts, which put further pressure on the population (Swanepoel et al., 2014).

Track surveys for guiding land-use planning

Overall, our models performed relatively well in inferring relationships between relative track density (as a proxy of species relative density) and environmental predictors, and our findings generally aligned with those in existing literature. Half a century ago, DHV (1980) identified three key factors influencing large herbivore distribution in the Kalahari: distribution of mineral nutrients in plants and soil, distribution of humans and livestock, and rainfall. In line with these factors, we also identified the importance of burned areas for most herbivores. Although the current fire regime is largely human-induced, spatially and temporally limited fires can be beneficial because they provide nutrient-rich regrowth, whereas large-scale fires are typically detrimental (Maabong & Mphale, 2021). Among the above-cited factors, cattleposts appear particularly important. The magnitude and variance of their effect across species likely depend on the tolerance of each species toward cattleposts, trade-offs with other resources, and the available sample size. Uncontrolled grazing by overstocked cattle herds often occurring in these areas reduces grass cover while increasing unpalatable grass and shrub density (Skarpe, 1986; Verlinden, 1997). Goats may further degrade browse quality (Bergström & Skarpe, 1999). These scenarios create unsuitable habitats for most large wild herbivores, particularly grazers. Vegetation degradation is typically observed within 10 km of cattleposts (Skarpe, 1986; Verlinden et al., 1998); however, we observed that gemsbok started appearing beyond 20 km, and eland presence increased steadily with distance. These findings may have resulted from hunting pressure (Senyatso, 2011; Thouless, 1998; Verlinden et al., 1998), as gemsbok and eland meat are particularly valued and frequently targeted by poachers in the Ghanzi district (Statistics Botswana, 2015; Thouless, 1998). Greater kudu, ostrich, and springbok tolerate human presence the most of the studied animals, whereas red hartebeest and blue wildebeest exhibit intermediate tolerance, apparently using livestock

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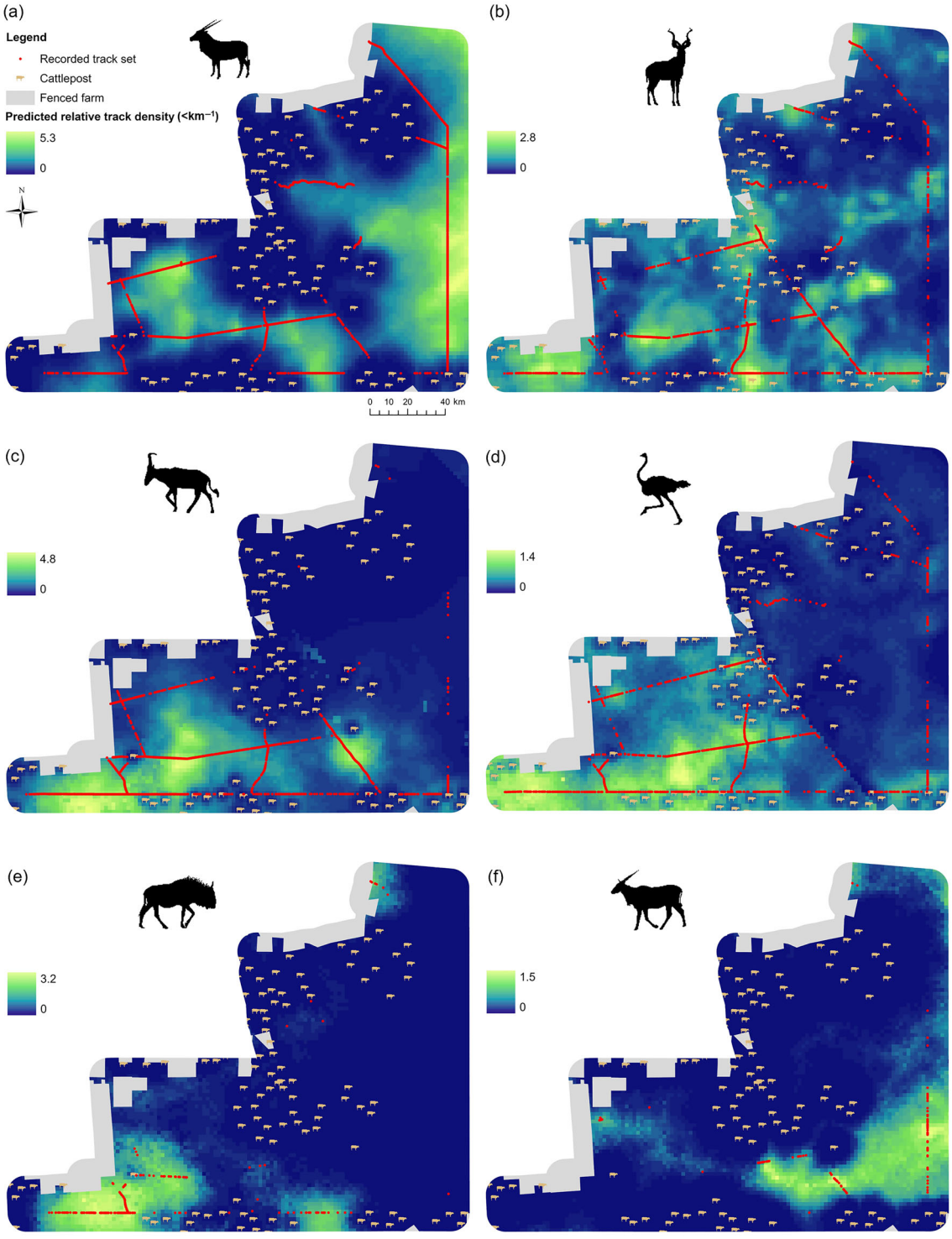


FIGURE 5 Predicted relative track densities per species, as proxies of relative animal densities, across the entire study area: (a) gemsbok, (b) greater kudu, (c) red hartebeest, (d) ostrich, (e) blue wildebeest, (f) eland, (g) springbok, (h) brown hyena, (i) leopard, (j) African wild dog, (k) cheetah, (l) lion, and (m) spotted hyena. To enhance the visual relevance of the results of the species maps, different data classification techniques were applied based on the shape of each species' data histogram. Natural breaks (Jenks) were used for gemsbok, red hartebeest, ostrich, and brown hyena. For greater kudu, eland, leopard, African wild dog, cheetah, and spotted hyena, manually densified natural breaks (Jenks) were employed to better represent high-frequency portions of the data. Quantile classification was used for blue wildebeest, springbok, and lion. Color gradients are only comparable within each map, not across maps, as predicted relative track density is a spatially explicit, species-specific relative measure for a given population size, and more mobile species are more likely to intersect transects, resulting in higher track density values. Maps also display the locations of cattleposts, fenced farms, and recorded track sets up to 6 days old. Icon sources: African wild dog, brown hyena, cheetah, leopard, and spotted hyena from PhyloPic (CC0 1.0). Greater kudu from PxHere Team (CC0 1.0). Springbok and eland by Robert Hering, gemsbok by T. Michael Keesey, and red hartebeest by Jan A. Venter, Herbert H. T. Prins, David A. Balfour, and Rob Slotow (vectorized by T. Michael Keesey) from PhyloPic (CC BY 3.0). Lion by Gabriela Palomo-Munoz and blue wildebeest by Graham Montgomery from PhyloPic (CC BY 4.0).

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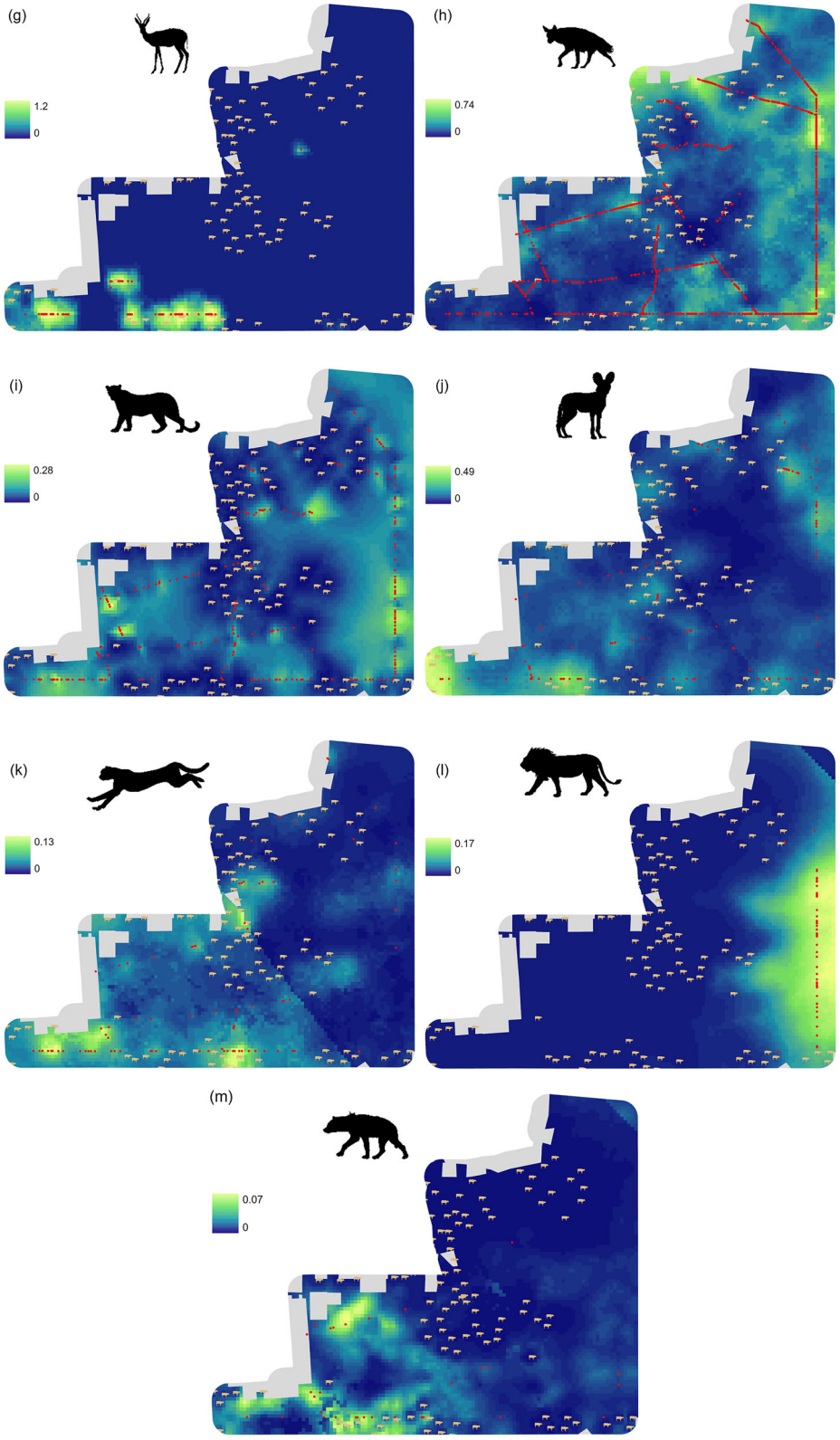


FIGURE 5 Continued

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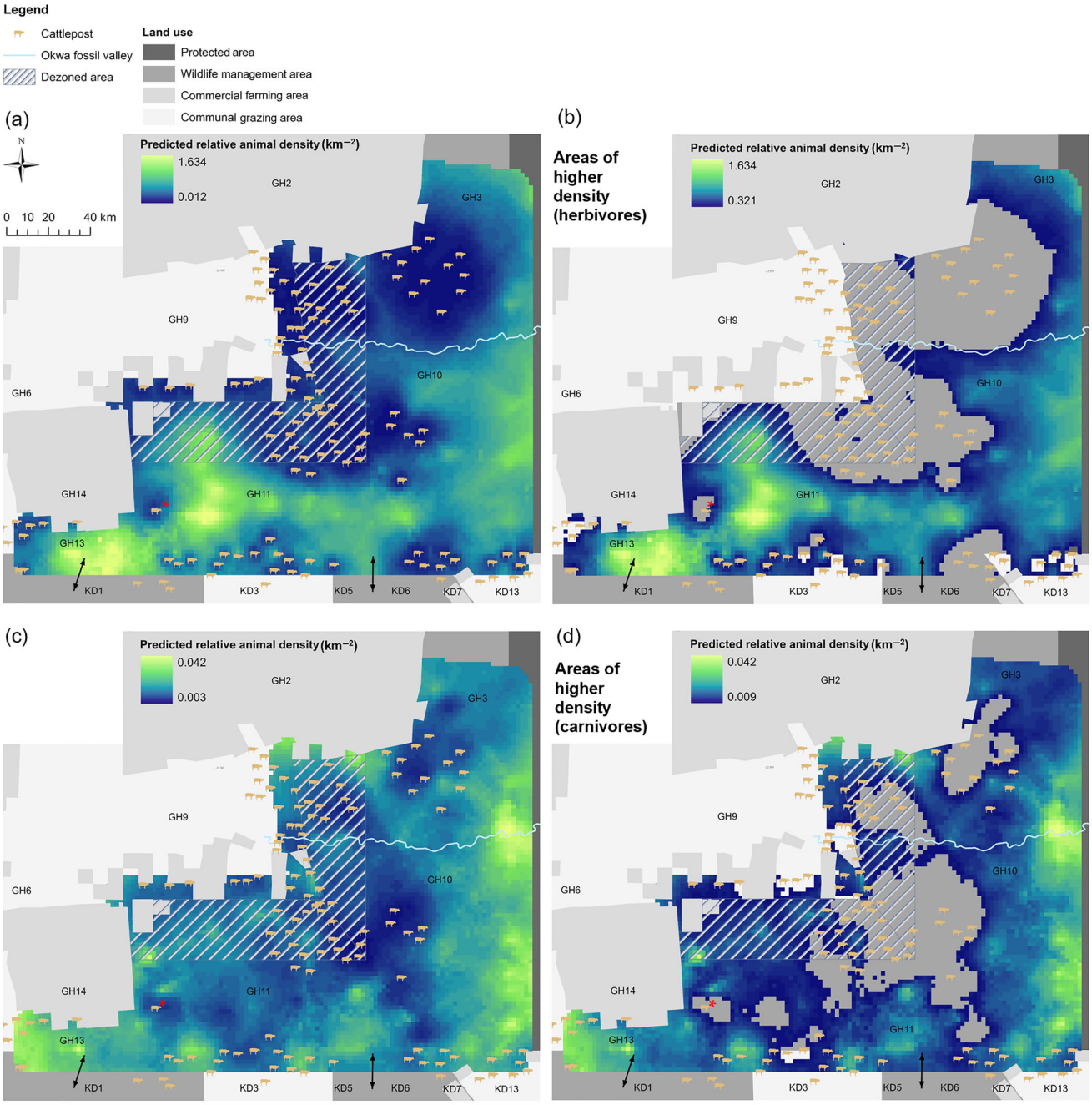


FIGURE 6 Relative animal density across the entire study area for (a) large herbivores and (c) large carnivores, with their respective estimated areas of higher relative density in (b) and (d). Data were classified with natural breaks (Jenks) for mapping. Color gradients are only comparable within each map, not across maps, as predicted relative animal density is a spatially explicit, guild-specific relative measure. The locations of cattleposts, land-use types, dezoned wildlife management areas for farming, and the Okwa fossil valley are also displayed to facilitate references in the discussion. The cattlepost marked with a red asterisk represents the settlement of Ranyane, established outside designated areas within GH11. The black arrow on the left indicates Corridor 1, whereas the arrow on the right marks Corridor 2—two of the three wildlife corridors identified by CI (2010) within the Western Kgalagadi Conservation Corridor area.

areas as transit zones between attractive resources (Ngwamotsoko, 1985). These characteristics may have contributed to the higher variance in cattlepost coefficients observed for some of these species. On the other hand, large carnivores are likely driven away by farmers who link them to livestock predation; African wild dogs, leopards, and lions are the most frequently reported conflict species in the region (Karunya Consulting et al., 2020; Statistics Botswana, 2021). African wild dogs nevertheless appeared to transit through cattlepost areas (Figure 5j), consistent with being the top conflict species.

Our results on relative wildlife density distribution also closely aligned with the comprehensive occurrence probability models in Keeping et al. (2022a) that were conducted across the WKCC, despite using independent track datasets (2008–2018)

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(see Appendix S20 for more detail on the temporal evolution for some species' distributions). Keeping et al. (2022b) predicted the complete loss of connectivity between the Central Kalahari Game Reserve and Kgalagadi Transfrontier Park for three disturbance-sensitive species—gemsbok, eland, and lion—if all proposed agricultural development was implemented. This development included cattleposts within the 20 km zone around WMA villages and the conversion of eastern GH10 and northern GH11 into fenced farms referred to as dezoned areas (Figure 6). To date, much of the cattlepost development around villages has been completed, leading to the apparent loss of connectivity for lions and potentially for eland as well (Figure 5f,l). Our results supported the land-use adjustments—primarily the realignment of some livestock zones—recommended by Keeping et al. (2022b) to preserve or restore connectivity (see Appendix S20 for more details). These recommendations were partially integrated into the ILUMP for the region (Tshukudu, 2025a, 2025b). The narrow pathway below Kacgae village, on the GH10–GH11 boundary, is critically important for potential movement to and from the Central Kalahari Game Reserve. Similarly, the small GH13 WMA, which supports several large pans, hosts one of the highest densities of large wildlife in the study area and forms the main potential route towards the Kgalagadi Transfrontier Park.

Methodologically, modeling improvements are possible. Surveyed cells had uneven transect lengths (median: 2.0 km, range: 0.006–4.368 km), with the shortest lengths potentially yielding unreliable track density estimates. Incorporating cell sampling effort as a covariate for track density variance—still under development in the sdmTMB R package—might address this issue. Models omitted interactions among individuals of the same species, though these may be more relevant for smaller-scale studies. Predation risk was also omitted from herbivore models, as resource availability in the Kalahari likely has a greater influence on large-scale herbivore distribution. Locally, herbivores adapt their behavior, such as seeking cover (e.g., greater kudu) or using open pans (e.g., blue wildebeest and red hartebeest). Finally, the FMP formula can be directly extended into a spatiotemporal Bayesian smoothing model to estimate variation in absolute population density over space and time (Jousimo & Ovaskainen, 2016). Although a promising approach, model convergence is sensitive to sparse data, a concern when relying solely on fresh tracks in a low-species-density system such as the Kalahari. However, the challenges associated with low-density species could be mitigated by increased sampling effort and survey repetition.

Track surveys with and for communities globally

A similar study could have been conducted using alternative methods such as camera trapping. However, this approach would have required an impractical number of camera traps and significantly higher costs (Keeping, Burger, et al., 2018; Seidlitz et al., 2021). In contrast, track surveys offer a key advantage by engaging local community members with advanced tracking skills. In addition to providing much-needed employment, track-based work also helps preserve and transmit these rapidly eroding skills, thereby valuing cultural identity and Indigenous knowledge (Aswani et al., 2018; Legge et al., 2024; Liebenberg, 2021). As with camera traps (e.g., Dickman et al., 2025), tracking could also be incorporated as a monitoring tool into conservation performance payment programs or used in other payments to encourage coexistence initiatives, thereby including trackers as an additional community group in conservation efforts. Benefiting directly from wildlife conservation and nurturing relationships with the rest of nature can potentially foster coexistence and renewed appreciation for wildlife (Dickman et al., 2011; Hamm et al., 2025; Jolly & Stronza, 2025). In the Kalahari, where climate change increasingly undermines the viability of cattle farming (Perkins, 2019), these initiatives, including tracking, offer a promising avenue for livelihood diversification (see Appendix S20). Such partnerships can potentially contribute to long-term ecological, cultural, and local economic benefits, while helping support land rights and promoting inclusive land management (IPBES, 2019; Liebenberg et al., 2017; Lilleyman et al., 2022).

Beyond the Kalahari, suitable tracking substrates (snow, mud, dust, and sand) and tracking knowledge are widely available. Tracking skills, for example, are present in countries such as Canada (Wong et al., 2011), Brazil (Dario, 2019), India (Lohe, 2014), and the Philippines (Hagen et al., 2016). A notable example of a track-based community project is the Arid Zone Monitoring Project in Australia, where Indigenous ranger groups have conducted sign-based species surveys across the country's deserts (3,273,140 km^2) over the past two decades (Legge et al., 2024). Although data collection currently focuses on the presence–absence of animal signs, testing the FMP approach to estimate absolute population density merits consideration. Indigenous peoples manage or hold tenure rights to over a quarter of the world's land surface, intersecting 40% of terrestrial PAs and ecologically intact landscapes (Garnett et al., 2018). Although not all seek to maintain the environment in its current state, their land management practices—usually rooted in a deep connection to the rest of nature—often align with and actively support biodiversity conservation. These factors highlight strong potential for the transferability of our approach and the development of conservation programs that integrate Indigenous knowledge in other regions, with track-based population monitoring as a key tool where substrates are suitable.

The FMP approach has been tested through several simulation studies and against other common field monitoring techniques, generating unbiased absolute population density estimates (Jousimo & Ovaskainen, 2016; Keeping & Pelletier, 2014; Keeping, Burger, et al., 2018; Stephens et al., 2006). However, these unbiased estimates are primarily contingent on the accuracy of $\hat{M}$ across both space and time (Prosekov et al., 2023; Stephens et al., 2006) and the ability to correct for the probability of track detection by observers when required (Gielen et al., 2024). Additionally, the confidence intervals of the density estimates remain relatively large, especially for rare, social, or territorial species, potentially complicating popula-

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tion trend assessments (Jousimo & Ovaskainen, 2016). Bayesian spatiotemporal extension of the FMP formula (Jousimo & Ovaskainen, 2016), as well as improved transect design and effort, could help address this issue. Despite these potential challenges, our work successfully demonstrated the broader applicability of track surveys using the FMP approach—a method replicable wherever suitable tracking substrates and skills are available—and their value in conservation and land-use planning.

With regard to the Kalahari, one might wonder why it deserves such attention, given the many other remarkable areas on Earth. As one of the largest remaining unfenced wilderness areas south of the Sahara, it challenges the traditional land-sparing model of isolated, self-sufficient PAs. Its multiuse areas hold as much, if not higher, value for some wildlife as those within protected boundaries (DWNP, 2015, 2018; Keeping, Keitsile, et al., 2018)—an observation applicable to many areas globally (Kremen, 2015). Therefore, such landscapes hold significant potential for a nature-based economy, which can coexist with agricultural land use through sustainable, system- and region-specific approaches (e.g., low-density, rotational cattle grazing in the Kalahari). Many of these regions also host incredible cultural heritages, with Indigenous knowledge developed over thousands of years, although rapidly disappearing (UN, 2011). However, efforts to preserve and sustainably develop such landscapes often falter due to complex interactions and diverging environmental, economic, and social interests (Hametner, 2022). Initiatives such as the Kalahari ILUMP represent an invaluable opportunity to integrate high-quality scientific data and input from various socioeconomic groups, including local communities, in order to increase the probability of implementation success. Comparable approaches exist in Canada (Ministry of Forests, 2021) and Australia (Andrews, 2025). Our study supports these efforts, and we encourage government bodies and stakeholders worldwide to lead by example in enforcing smart land-use planning that benefits both ecosystems and the well-being of the communities dependent on them over the long term.

AUTHOR CONTRIBUTIONS

M.-C.G. conceived the ideas and designed the surveys. M.-C.G., X.J., N.K., G.K., H.L., and Z.Z. collected the data. M.-C.G. processed the data. M.-C.G. analyzed the data with the help of V.R. and N.S. M.-C.G. created the artwork and led the writing of the manuscript, and V.R. and N.S. revised it. M.-G.C. and N.S. acquired the funding. N.S. supervised the study. M.-C.G. is a Research Fellow, and N.S. is an honorary Senior Research Associate of the Fonds de la Recherche Scientifique (FNRS). Our study brought together authors from several countries, including expert trackers based locally. Their consent for publication was obtained by orally explaining the study conclusions, due to limited familiarity with written scientific English. Extended fieldwork fostered extensive knowledge exchange among team members. MCG and younger trackers learned from Master Trackers and completed their CyberTracker certification. Results were shared with the Government of Botswana and local communities to support wildlife management and land-use planning decisions.

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DATA AVAILABILITY STATEMENT

Data are co-owned by UCLouvain and Cheetah Conservation Botswana. The datasets analyzed during the current study are available from the corresponding author on request. Example R scripts and associated sample data detailing sdmTMB modeling workflows are available in Appendices S7–S18.

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REFERENCES

Abrahms, B., Jordan, N. R., Golabek, K. A., McNutt, J. W., Wilson, A. M., & Brashares, J. S. (2016). Lessons from integrating behaviour and resource selection: Activity-specific responses of African wild dogs to roads. *Animal Conservation*, *19*(3), 247–255. https://doi.org/10.1111/acv.12235

Ahlswede, S., Fabiano, E. C., Keeping, D., & Birkhofer, K. (2019). Using the Formozov–Malyshev–Pereleshin formula to convert mammal spoor counts into density estimates for long-term community-level monitoring. *African Journal of Ecology*, *57*(2), 177–189. https://doi.org/10.1111/aje.12587

Anderson, S. C., Ward, E. J., English, P. A., Barnett, L. A. K., & Thorson, J. T. (2024). sdmTMB: An R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. *BioRxiv*, 485545. https://doi.org/10.1101/2022.03.24.485545

Anderson, S. C., Ward, E. J., English, P. A., Barnett, L. A. K., & Thorson, J. T. (2026). *Cross-validation for model evaluation and comparison*. https://sdmtmb.github.io/sdmTMB/articles/cross-validation.html

Andrews, K. (2025). Everything is connected—Why Australia needs integrated landscape management. *Australian Environment Review*, *39*(1/2), 13–17.

Aswani, S., Lemahieu, A., & Sauer, W. H. H. (2018). Global trends of local ecological knowledge and future implications. *PLoS ONE*, *13*(4), Article e0195440. https://doi.org/10.1371/journal.pone.0195440

Batisani, N., & Yarnal, B. (2010). Rainfall variability and trends in semi-arid Botswana: Implications for climate change adaptation policy. *Applied Geography*, *30*(4), 483–489. https://doi.org/10.1016/j.apgeog.2009.10.007

Bergström, R., & Skarpe, C. (1999). The abundance of large wild herbivores in a semi-arid savanna in relation to seasons, pans and livestock. *African Journal of Ecology*, *37*(1), 12–26. https://doi.org/10.1046/j.1365-2028.1999.00165.x

15231739, 0, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.70397 by Marie-Charlotte Gielen , Wiley Online Library on [01/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Bond , I., Child, B., de la Harpe , D., Jones , B., Barnes , J., & Anderson, H. (2004). Private land contribution to conservation in South Africa. In B. Child (Ed.), *Parks in transition: Biodiversity, rural development and the bottom line* (1st ed., pp. 29–61). Earthscan.

Bonifica. (1992). *Initial measures for the conservation of the Kalahari ecosystem: Final report*. Bonifica Iritecna, Gruppo IRI.

Bothma, J. d. P., & Walker, C. (1999). *Larger carnivores of the African Savannas*. Springer.

Carbone, C., Cowlishaw, G., Isaac, N. J. B., & Rowcliffe, J. M. (2005). How far do animals go? Determinants of day range in mammals. *The American Naturalist*, *165*(2), 290–297. https://doi.org/10.1086/426790

Chelintsev, N. G. (1995). Mathematical principles of winter censuses of mammals. *Byulleten Moskovskogo Obschestva Ispytatelei Prirody*, *100*, 3–19.

Chen, Y., & Gillieson, D. (2009). Evaluation of Landsat TM vegetation indices for estimating vegetation cover on semi-arid rangelands: A case study from Australia. *Canadian Journal of Remote Sensing*, *35*(5), 435–446. https://doi.org/10.5589/m09-037

Child, G. (1972). Observations on a wildebeest die-off in Botswana. *Arnoldia (Rhodesia)*, *5*(31), 1–13.

Conservation International (CI). (2010). *Consultancy to identify important habitats for key wildlife in the Western Kgalagadi Conservation Corridor (WKCC)*. Author.

Cooke, H. J. (1985). The Kalahari today: A case of conflict over resource use. *The Geographical Journal*, *151*(1), 75–85. https://doi.org/10.2307/633282

DG Ecological Consulting. (2010). Animal distribution, numbers and trends in the Kalahari ecosystem 1989-2005: A report to the Kalahari Ecosystems Corridor Project. Author.

Dario, F. R. (2019). The relationship between Bororo Indigenous and the wildlife in the Brazilian Savannah. *World News of Natural Sciences*, *24*, 239–249.

DHV. (1980). *Countrywide animal and range assessment project: Final report* (7 volumes). DHV Consulting Engineers.

Dickman, A., Cotterill, A., Asecheka, S., Mlaponi, Z., Mbugi, H., Grau, A., … & Cascio, B. (2025). Community camera trapping: A novel method for encouraging human–big cat coexistence on human-dominated land. *Wildlife Letters*, *3*(1), 22–29. https://doi.org/10.1002/wll2.70006

Dickman, A. J., Macdonald, E. A., & Macdonald, D. W. (2011). A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. *Proceedings of the National Academy of Sciences*, *108*(34), 13937–13944. https://doi.org/10.1073/pnas.1012972108

Department of Meteorological Services (DMS). (2021). Daily rainfall data from meteorological stations of the Ghanzi District and Kgalagadi North District. Years 2018-2021. Author.

Doran-Myers, D., Kenney, A. J., Krebs, C. J., Lamb, C. T., Menzies, A. K., Murray, D., … & Boutin, S. (2021). Density estimates for *Canada lynx* vary among estimation methods. *Ecosphere*, *12*(10), Article e03774. https://doi.org/10.1002/ecs2.3774

Dröge, E., Creel, S., Becker, M. S., Loveridge, A. J., Sousa, L. L., & Macdonald, D. W. (2020). Assessing the performance of index calibration survey methods to monitor populations of wide-ranging low-density carnivores. *Ecology and Evolution*, *10*(7), 3276–3292. https://doi.org/10.1002/ece3.6065

Department of Wildlife and National Parks (DWNP). (2015). Aerial survey of animals in south-west Botswana—Dry season 2015. Author.

Department of Wildlife and National Parks (DWNP). (2018). Botswana Wildlife Aerial Survey—Dry season 2018. Author.

Esbach, M. S. (2023). Estimating mammal density from track counts collected by Indigenous Amazonian hunters. *Perspectives in Ecology and Conservation*, *21*(3), 247–252. https://doi.org/10.1016/j.pecon.2023.07.005

Formozov, A. (1932). Formula for quantitative censusing of mammals by tracks. *Russian Journal of Zoology*, *11*, 66–69.

Garnett, S. T., Burgess, N. D., Fa, J. E., Fernández-Llamazares, Á., Molnár, Z., Robinson, C. J., … & Leiper, I. (2018). A spatial overview of the global importance of Indigenous lands for conservation. *Nature Sustainability*, *1*(7), 369–374. https://doi.org/10.1038/s41893-018-0100-6

Gielen, M.-C., Araldi, A., Jardeaux, M., Pule, S., Mosolelo, S., Seganaphohu, X. F., … & Schtickzelle, N. (2025). Refining population density estimation from track counts: Improving daily travel distance estimates through trailing of large herbivores in the Kalahari, Botswana. *Movement Ecology*, *13*, Article 53. https://doi.org/10.1186/s40462-025-00582-1

Gielen, M.-C., Johannes, X., Kashe, N., Khumo, G., Zoronxhogo, Z., & Schtickzelle, N. (2024). Monitoring wildlife abundance through track surveys: A capture-mark-recapture inspired approach to assess track detection by certified trackers in the Kalahari, Botswana. *Global Ecology and Conservation*, *51*, Article e02924. https://doi.org/10.1016/j.gecco.2024.e02924

Government of Botswana. (1986). Wildlife Conservation Policy (A paper on the utilization of the wildlife resource of Botswana on a sustainable basis)—Government paper 1 of 1986. Author.

Government of Botswana. (2024). Public notice as per Wildlife Conservation and National Parks Act (Act n°28 of 1992): Wildlife hunting quota 2025. Department of Wildlife and National Parks.

Gu, J., Yu, L., Hua, Y., Ning, Y., Heng, B., Qi, J., … & Li, Z. (2018). A comparison of food habits and prey preferences of Amur tiger (*Panthera tigris altaica*) at the southwest Primorskii Krai in Russia and Hunchun in China. *Integrative Zoology*, *13*(5), 595–603. https://doi.org/10.1111/1749-4877.12322

Hagen, R., van der Ploeg, J., & Minter, T. (2016). How do hunter-gatherers learn? The transmission of indigenous knowledge among the Agta of The Philippines. *Hunter Gatherer Research*, *2*(4), 389–413. https://doi.org/10.3828/hgr.2016.27

Hägerling, H. G., & Ebersole, J. J. (2017). Roads as travel corridors for mammals and ground birds in Tarangire National Park, Tanzania. *African Journal of Ecology*, *55*(4), 701–704. https://doi.org/10.1111/aje.12386

Hametner, M. (2022). Economics without ecology: How the SDGs fail to align socioeconomic development with environmental sustainability. *Ecological Economics*, *199*, Article 107490.

Hamm, J., Holmes, G., Mabele, M. B., & Martin-Ortega, J. (2025). "Milking the lions": An analysis of conservation performance payments in eastern and southern Africa. *Conservation Science and Practice*, *7*(3), Article e70015. https://doi.org/10.1111/csp2.70015

Hayward, M. W., Boitani, L., Burrows, N. D., Funston, P. J., Karanth, K. U., MacKenzie, D. I., … & Yarnell, R. W. (2015). FORUM: Ecologists need robust survey designs, sampling and analytical methods. *Journal of Applied Ecology*, *52*(2), 286–290. https://doi.org/10.1111/1365-2664.12408

Hempson, G. P., Archibald, S., & Bond, W. J. (2017). The consequences of replacing wildlife with livestock in Africa. *Scientific Reports*, *7*, Article 17196. https://doi.org/10.1038/s41598-017-17348-4

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). (2018). *The IPBES regional assessment report on biodiversity and ecosystem services for Africa*. IPBES Secretariat.

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). (2019). *Global assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. IPBES Secretariat.

Jolly, H., & Stronza, A. (2025). Insights on human–wildlife coexistence from social science and Indigenous and traditional knowledge. *Conservation Biology*, *39*(2), Article e14460. https://doi.org/10.1111/cobi.14460

Jousimo, J., & Ovaskainen, O. (2016). A spatio-temporally explicit random encounter model for large-scale population surveys. *PLoS ONE*, *11*(9), Article e0162447. https://doi.org/10.1371/journal.pone.0162447

Karanth, K. U., Nichols, J. D., Seidenstricker, J., Dinerstein, E., Smith, J. L. D., McDougal, C., … & Thapar, V. (2003). Science deficiency in conservation practice: The monitoring of tiger populations in India. *Animal Conservation*, *6*(2), 141–146. https://doi.org/10.1017/S1367943003003184

Karunya Consulting, Cheetah Conservation Botswana, & Kalahari Research and Conservation. (2020). *Final scoping report: Research on human-wildlife conflict in the Kalahari landscape. Under UNDP Kgalagadi & Ghanzi Drylands Ecosystem Project: Managing the human-wildlife interface to sustain the flow of agro-ecosystem services and prevent illegal trafficking in the Kgalagadi and Ghanzi Drylands*. Karunya Consulting.

Keeping, D. (2014). Rapid assessment of wildlife abundance: Estimating animal density with track counts using body mass–day range scaling rules. *Animal Conservation*, *17*(5), 486–497. https://doi.org/10.1111/acv.12113

Keeping, D., Burger, J. H., Keitsile, A. O., Gielen, M.-C., Mudongo, E., Wallgren, M., … & Foote, A. L. (2018). Can trackers count free-ranging wildlife as effectively and efficiently as conventional aerial survey and distance sampling? Implications for citizen science in the Kalahari, Botswana. *Biological Conservation*, *223*, 156–169. https://doi.org/10.1016/j.biocon.2018.04.027

15231739, 0, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.70397 by Marie-Charlotte Gielen , Wiley Online Library on [01/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Keeping, D., Kaszta, Z., & Cushman, S. A. (2022a). *Kalahari Wildlife Landscape Connectivity Analysis—Phase 1 Report*. United Nations Development Programme (UNDP) Kgalagadi-Ghanzi Drylands Ecosystem Project.

Keeping, D., Kaszta, Z., & Cushman, S. A. (2022b). *Kalahari Wildlife Landscape Connectivity Analysis—Phase 2 (Final) Report*. United Nations Development Programme (UNDP) Kgalagadi-Ghanzi Drylands Ecosystem Project.

Keeping, D., Keitsile, A. O., & Burger, J. H. (2018). Eland in Botswana's Kalahari: Now the largest free-ranging population in Africa? *Gnusletter*, *35*(1), 21–26.

Keeping, D., & Pelletier, R. (2014). Animal density and track counts: Understanding the nature of observations based on animal movements. *PLoS ONE*, *9*(5), Article e96598. https://doi.org/10.1371/journal.pone.0096598

Klein, R. A. (2013). An assessment of human carnivore conflict in the Kalahari region of Botswana (MSc thesis). Rhodes University.

Kondratenkov, I. A. (2019). Some aspects of the theory of winter route counting of game animals. *Biology Bulletin*, *46*(10), 1211–1223. https://doi.org/10.1134/S1062359019100169

Kremen, C. (2015). Reframing the land-sparing/land-sharing debate for biodiversity conservation. *Annals of the New York Academy of Sciences*, *1355*(1), 52–76. https://doi.org/10.1111/nyas.12845

Lancaster, I. N. (1974). Pans of the Southern Kalahari. *Botswana Notes and Records*, *6*, 157–169. http://www.jstor.org/stable/40959216

Legge, S., Indigo, N., Southwell, D. M., Skroblin, A., Nou, T., Young, A. R., … & Backhouse, B. (2024). The Arid Zone Monitoring Project: Combining Indigenous ecological expertise with scientific data analysis to assess the potential of using sign-based surveys to monitor vertebrates in the Australian deserts. *Wildlife Research*, *51*(9), Article WR24070. https://doi.org/10.1071/WR24070

Liebenberg, L. (2021). *The origin of science* (2nd ed.). CyberTracker.

Liebenberg, L., Steventon, J., Brahman, N., Benadie, K., Minye, J., Langwane, H. K., & Xhukwe, Q. U. (2017). Smartphone Icon User Interface design for non-literate trackers and its implications for an inclusive citizen science. *Biological Conservation*, *208*, 155–162. https://doi.org/10.1016/j.biocon.2016.04.033

Lilleyman, A., Millar, G., Burn, S., Fatt, K. H.-L., Talbot, A., Que-Noy, J., … & Smith, B. C. D. (2022). Indigenous knowledge in conservation science and the process of a two-way research collaboration. *Conservation Science and Practice*, *4*(8), Article e12727. https://doi.org/10.1111/csp2.12727

Lindsey, P. A., Alexander, R., Mills, M. G. L., Romañach, S., & Woodroffe, R. (2007). Wildlife viewing preferences of visitors to protected areas in South Africa: Implications for the role of ecotourism in conservation. *Journal of Ecotourism*, *6*(1), 19–33. https://doi.org/10.2167/joe133.0

Lindsey, P. A., Frank, L. G., Alexander, R., Mathieson, A., & Romañach, S. S. (2007). Trophy hunting and conservation in Africa: Problems and one potential solution. *Conservation Biology*, *21*(3), 880–883. https://doi.org/10.1111/j.1523-1739.2006.00594.x

Lohe, N. (2014). Traditional knowledge system in hunting and trapping methods among the Nagas of northeast India. *Asian Journal of Multidisciplinary Studies*, *2*(8), 184–189.

Maabong, K. E., & Mphale, K. (2021). Wildfires in Botswana and their frequency of occurrence. *Atmospheric and Climate Sciences*, *11*(4), 689–696. https://doi.org/10.4236/acs.2021.114040

Maidment, R. I., Grimes, D., Allan, R. P., Tarnavsky, E., Stringer, M., Hewison, T., … & Black, E. (2014). The 30 year TAMSAT African Rainfall Climatology And Time series (TARCAT) data set. *Journal of Geophysical Research: Atmospheres*, *119*(18), 10,619–10,644. https://doi.org/10.1002/2014JD021927

Maidment, R. I., Grimes, D., Black, E., Tarnavsky, E., Young, M., Greatrex, H., … & Alcántara, E. M. U. (2017). A new, long-term daily satellite-based rainfall dataset for operational monitoring in Africa. *Scientific Data*, *4*(1), Article 170063. https://doi.org/10.1038/sdata.2017.63

Malhi, Y., Doughty, C. E., Galetti, M., Smith, F. A., Svenning, J.-C., & Terborgh, J. W. (2016). Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proceedings of the National Academy of Sciences*, *113*(4), 838–846. https://doi.org/10.1073/pnas.1502540113

Mills, M. G. L. (1984). Prey selection and feeding habits of the large carnivores in the Southern Kalahari. *Koedoe*, *27*(2), 281–294. https://doi.org/10.4102/koedoe.v27i2.586

Mills, M. G. L. (1990). *Kalahari hyaenas: Comparative behavioural ecology of two species*. Springer.

Ministry of Forests. (2021). *Modernized land use planning: A guide to effective stakeholder engagement*. The Ministry of Forests, Lands, Natural Resource Operations and Rural Development.

Ministry of Local Government. (2009). *Revised Remote Area Development Programme (RADP)*. Government of Botswana.

Ngwamotsoko, K. T. (1985). Large animals and land resources of Western Central Kalahari, Botswana (MSc thesis). University of New England.

Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., & Balkenhol, N. (2019). Validating movement corridors for African elephants predicted from resistance-based landscape connectivity models. *Landscape Ecology*, *34*(4), 865–878. https://doi.org/10.1007/s10980-019-00811-0

Packer, C., Kosmala, M., Cooley, H. S., Brink, H., Pintea, L., Garshelis, D., … & Nowell, K. (2009). Sport hunting, predator control and conservation of large carnivores. *PLoS ONE*, *4*(6), Article e5941. https://doi.org/10.1371/journal.pone.0005941

Parris, R., & Child, G. (1973). The importance of pans to wildlife in the Kalahari and the effect of human settlement on these areas. *Journal of Southern African Wildlife Management Association*, *3*(1), 1–8. https://hdl.handle.net/10520/AJA03794369_3442

Parry, D. C., & Campbell, B. M. (1990). Wildlife management areas of Botswana. *Botswana Notes and Records*, *22*, 65–77. http://www.jstor.org/stable/40979856

Perkins, J. S. (1996). Botswana: Fencing out the equity issue. Cattleposts and cattle ranching in the Kalahari Desert. *Journal of Arid Environments*, *33*(4), 503–517. https://doi.org/10.1006/jare.1996.0086

Perkins, J. S. (2019). 'Only connect': Restoring resilience in the Kalahari ecosystem. *Journal of Environmental Management*, *249*, Article 109420. https://doi.org/10.1016/j.jenvman.2019.109420

Perkins, S. G. (2011). Track data analysis indicating the distribution and movement patterns of eastern coyote (*Canis* latrans) on a Cape Cod barrier beach. BSc thesis. Wheaton College, Massachusetts.

Popova, E. D., Ahmed, A. A., Genov, P. V., Hodzha, M. M., & Zlatanova, D. P. (2019). Estimating population density of roe deer *Capreolus capreolus* (L.) (Artiodactyla: Cervidae) for better management: Comparison of three methods. *Acta Zoologica Bulgarica*, *71*(4), 531–536.

Prosekov, A. Y., Kaledin, A. P., Beketov, S. V., Golubeva, O. N., & Ostapchuk, A. M. (2023). Modern methods of carrying out a census of game animals. *Biology Bulletin Reviews*, *13*(3), S286–S300. https://doi.org/10.1134/S2079086423090086

Purevdorj, T. S., Tateishi, R., Ishiyama, T., & Honda, Y. (1998). Relationships between percent vegetation cover and vegetation indices. *International Journal of Remote Sensing*, *19*(18), 3519–3535. https://doi.org/10.1080/014311698213795

Qi, J., Chehbouni, A., Huete, A. R., Kerr, Y. H., & Sorooshian, S. (1994). A modified soil adjusted vegetation index. *Remote Sensing of Environment*, *48*(2), 119–126. https://doi.org/10.1016/0034-4257(94)90134-1

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., … & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), Article 1241484. https://doi.org/10.1126/science.1241484

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., … & Lindsey, P. A. (2015). Collapse of the world's largest herbivores. *Science Advances*, *1*(4), Article e1400103. https://doi.org/10.1126/sciadv.1400103

Romani, T., Giannone, C., Mori, E., & Filacorda, S. (2018). Use of track counts and camera traps to estimate the abundance of roe deer in North-Eastern Italy: Are they effective methods? *Mammal Research*, *63*(4), 477–484. https://doi.org/10.1007/s13364-018-0386-9

Seidlitz, A., Bryant, K. A., Armstrong, N. J., Calver, M. C., & Wayne, A. F. (2021). Sign surveys can be more efficient and cost effective than driven transects and camera trapping: A comparison of detection methods for a small elusive mammal, the numbat (*Myrmecobius fasciatus*). *Wildlife Research*, *48*(6), 491–500. https://doi.org/10.1071/WR20020

Senyatso, K. (2011). Conserving widely distributed wildlife species in an African savanna: Parks, cattle-grazing and community-managed areas (PhD thesis). University of East Anglia.

15231739, 0, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.70397 by Marie-Charlotte Gielen , Wiley Online Library on [01/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Skarpe, C. (1980). Observations on two bushfires in the western Kalahari, Botswana. In E. Sjogren (Ed.), *Studies in plant ecology*, (Vol. 68, pp. 131–140). Acta Phytogeographica Suecica.

Skarpe, C. (1986). Plant community structure in relation to grazing and environmental changes along a north-south transect in the western Kalahari. *Vegetatio*, *68*(1), 3–18. https://doi.org/10.1007/BF00031575

Smithers, R. H. N. (1971). The mammals of Botswana (PhD thesis). University of Pretoria.

Southgate, R., Paltridge, R., Masters, P., & Carthew, S. (2007). Bilby distribution and fire: A test of alternative models of habitat suitability in the Tanami Desert, Australia. *Ecography*, *30*(6), 759–776. https://doi.org/10.1111/j.2007.0906-7590.04956.x

Statistics Botswana. (2015). Botswana Environment Statistics: Wildlife Digest 2014. Author.

Statistics Botswana. (2021). Botswana Selected Environmental Indicators Digest *2020*. Author.

Stephens, P. A., Vieira, M. V., Willis, S. G., & Carbone, C. (2019). The limits to population density in birds and mammals. *Ecology Letters*, *22*(4), 654–663. https://doi.org/10.1111/ele.13227

Stephens, P. A., Zaumyslova, O. Y., Miquelle, D. G., Myslenkov, A. I., & Hayward, G. D. (2006). Estimating population density from indirect sign: Track counts and the Formozov–Malyshev–Pereleshin formula. *Animal Conservation*, *9*(3), 339–348. https://doi.org/10.1111/j.1469-1795.2006.00044.x

Swanepoel, L., Lindsey, P., Somers, M., van Hoven, W., & Dalerum, F. (2014). The relative importance of trophy harvest and retaliatory killing of large carnivores: South African leopards as a case study. *South African Journal of Wildlife Research*, *44*(2), 115–134. https://doi.org/10.3957/056.044.0210

Tarnavsky, E., Grimes, D., Maidment, R., Black, E., Allan, R. P., Stringer, M., … & Kayitakire, F. (2014). Extension of the TAMSAT satellite-based rainfall monitoring over Africa and from 1983 to present. *Journal of Applied Meteorology and Climatology*, *53*(12), 2805–2822. https://doi.org/10.1175/JAMC-D-14-0016.1

Thorn, M., Green, M., Bateman, P. W., Waite, S., & Scott, D. M. (2011). Brown hyaenas on roads: Estimating carnivore occupancy and abundance using spatially auto-correlated sign survey replicates. *Biological Conservation*, *144*(6), 1799–1807. https://doi.org/10.1016/j.biocon.2011.03.009

Thouless, C. R. (1998). Large mammals inside and outside protected areas in the Kalahari. *Transactions of the Royal Society of South Africa*, *53*(2), 245–255. https://doi.org/10.1080/00359199809520391

Tshukudu, K. (2025a). Integrated Land Use Management Plan (ILUMP) for Ghanzi and Charleshill Districts. Government of Botswana and the United Nations Development Programme (UNDP), Gaborone.

Tshukudu, K. (2025b). Integrated Land Use Management Plan (ILUMP) for Tsabong and Hukuntsi Districts. Government of Botswana and the United Nations Development Programme (UNDP), Gaborone.

Tyson, P. D. (1980). Temporal and spatial variation of rainfall anomalies in Africa south of latitude 22 during the period of meteorological record. *Climatic Change*, *2*(4), 363–371. https://doi.org/10.1007/BF00137205

United Nations (UN). (2011). *State of the world's Indigenous peoples*. https://doi.org/10.18356/e92ca6a3-en

UN Environment Programme World Conservation Monitoring Centre (UNEP-WCMC), & International Union for Conservation of Nature (IUCN). (2025). *The World Database on Protected Areas (WDPA)*. www.protectedplanet.net

Van der Weyde, L. K. (2019). *Cattle spatial use at cattle posts in Wildlife Management Areas—Research Report 19.5*. Cheetah Conservation Botswana.

Van der Weyde, L. K., Theisinger, O., Mbisana, C., Gielen, M.-C., & Klein, R. (2021). The value of pastoral ranches for wildlife conservation in the Kalahari. *Wildlife Research*, *49*(3), 215–226. https://doi.org/10.1071/WR21048

Van der Weyde, L. K., Tobler, M. W., Gielen, M. C., Cozzi, G., Weise, F. J., Adams, T., … & Brassine, A. (2022). Collaboration for conservation: Assessing countrywide carnivore occupancy dynamics from sparse data. *Diversity and Distributions*, *28*(5), 917–929. https://doi.org/10.1111/ddi.13386

van Rooyen, N., & van Rooyen, M. W. (1998). Vegetation of the south-western arid Kalahari: An overview. *Transactions of the Royal Society of South Africa*, *53*(2), 113–140. https://doi.org/10.1080/00359199809520381

Verlinden, A. (1997). Human settlements and wildlife distribution in the southern Kalahari of Botswana. *Biological Conservation*, *82*(2), 129–136.

Verlinden, A., & Masogo, R. (1997). Satellite remote sensing of habitat suitability for ungulates and ostrich in the Kalahari of Botswana. *Journal of Arid Environments*, *35*(3), 563–574. https://doi.org/10.1006/jare.1996.0174

Verlinden, A., Perkins, J. S., Murray, M., & Masunga, G. (1998). How are people affecting the distribution of less migratory wildlife in the southern Kalahari of Botswana? A spatial analysis. *Journal of Arid Environments*, *38*(1), 129–141. https://doi.org/10.1006/jare.1997.0298

Waller, S. J., Hebblewhite, M., Brodie, J. F., Soutyrina, S. V., & Miquelle, D. G. (2024). Cameras or Camus? Comparing snow track surveys and camera traps to estimate densities of unmarked wildlife populations. *Ecology and Evolution*, *14*(12), Article e70747. https://doi.org/10.1002/ece3.70747

Wildlife Conservation Society (WCS), & Columbia University Center for International Earth Science Information Network (CIESIN). (2005). *Last of the Wild Project, Version 2, 2005 (LWP-2): Last of the Wild Dataset (Geographic)*. NASA Socioeconomic Data and Applications Center (SEDAC).

Weare, P. R., & Yalala, A. (1971). Provisional vegetation map of Botswana. *Botswana Notes and Records*, *3*, 131–147. http://www.jstor.org/stable/40979284

Williamson, D., Williamson, J., & Ngwamotsoko, K. T. (1988). Wildebeest migration in the Kalahari. *African Journal of Ecology*, *26*(4), 269–280. https://doi.org/10.1111/j.1365-2028.1988.tb00979.x

Winkler, K., Fuchs, R., Rounsevell, M., & Herold, M. (2021). Global land use changes are four times greater than previously estimated. *Nature Communications*, *12*, Article 2501. https://doi.org/10.1038/s41467-021-22702-2

Wong, P. B. Y., de Groot, P. V. C., Fekken, C., Smith, H., Pages, M., & Boag, P. T. (2011). Interpretations of polar bear (*Ursus maritimus*) tracks by Inuit hunters: Inter-rater reliability and inferences concerning accuracy. *The Canadian Field-Naturalist*, *125*(2), 140–153. https://doi.org/10.22621/cfn.v125i2.1197

Yuling, Y., Aki, V., Daniel, S., & Andrew, G. (2018). Using stacking to average Bayesian predictive distributions (with Discussion). *Bayesian Analysis*, *13*(3), 917–1007. https://doi.org/10.1214/17-BA1091

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