

Chapter 5

Integrating Indigenous knowledge and modern technology to model wildlife density and potential movement based on animal track counts.

Marie-Charlotte Gielen^{a,b,*}, Xiko Johannes^c, Njoxlau Kashe^d, Glam Khumo^d,
Horekwe (Karooha) Langwane^{e†}, Zoro Zoronxhogo^c, Viktoriia Radchuk^f,
Nicolas Schtickzelle^a.

^aEarth and Life Institute, Université catholique de Louvain, Louvain-la-Neuve, Belgium

^bConservation Research Department, Cheetah Conservation Botswana, Gaborone, Botswana

^cEast Hanahai, Botswana

^dBere, Botswana

^eKacgae, Botswana

^fLeibniz Institute for Zoo and Wildlife Research, Berlin, Germany

[†]Deceased

*Corresponding author: marie-charlotte.gielen@uclouvain.be, mariecharlotte.gielen@gmail.com

Acknowledgements

The authors would like to thank the Government of Botswana via the Department of Wildlife and National Parks and the Ministry of Environment, Natural Resources Conservation and Tourism for permissions to conduct this research (Permit number: EWT 8/36/4 XXXVIII (37, 38, 39)). M.-C.G. also express her profound gratitude to the Ghanzi District tracker community for partnering with her and making the field work possible; she admires their discipline and hard work throughout the long days spent in the bush, their enthusiasm towards the natural world, and their humble custodianship of the knowledge they agreed to share. A special tribute goes to the late Master Tracker Horekwe (Karooha) Langwane for the invaluable legacy he has left behind. M.-C.G. further thanks Cheetah Conservation Botswana for logistic support, Kanabo Conservation Link for lending field equipment, and especially Derek Keeping for his ongoing guidance on track survey protocols and analysis. Finally, the authors thank Leanne Van der Weyde for sharing useful insights into species distribution models.

Funding

M.-C.G. is a Research Fellow and N.S. a Senior Research Associate of the Fonds de la Recherche Scientifique – FNRS. This work was supported by the Fonds de la Recherche Scientifique – FNRS under Grant No CDR J.0184.20.

Authorship contribution

MCG conceived the ideas and designed the surveys; MCG, XJ, NK, GK, HL, ZZ collected the data; MCG processed the data; MCG analysed the data with the help of VR, NS; MCG created the artwork and led the writing of the manuscript and VR and NS revised it. MCG and NS acquired the funding. NS supervised the study. All authors contributed critically to the study and gave final approval for publication. Our study brings together authors from several countries, including expert trackers based in the country where the study was carried out.

Ethical standards

The research involved non-invasive wildlife surveys of indirect animal signs, therefore ethics and animal welfare approvals were not required.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on request.

Abstract

The UN Convention on Biological Diversity recently set a global target to conserve and manage 30% of the Earth's land by 2030. In this context, Botswana's Kalahari hosts one of sub-Saharan Africa's largest unprotected areas supporting free-ranging wildlife — the Western Kgalagadi Conservation Corridor (WKCC). However, its role as both wildlife habitat and movement corridor is increasingly threatened by land-use change. This study provides updated, fine-scale insights into large wildlife species in the northern WKCC with three main objectives: (1) Estimate their population densities, (2) identify key predictors of their spatial variation, and (3) derive predictive maps to highlight higher wildlife density and potential movement pathways. Leveraging the Kalahari's sandy substrate and Indigenous tracking skills, we conducted biannual animal track survey over three years across 22,000km² of multi-use Wildlife Management Areas between two protected areas. While track data are often limited to presence-absence information, we demonstrate a more comprehensive application by analyzing 22,793 tracks from 13 herbivore and carnivore species. Absolute abundance estimates were derived using the Formozov-Malyshv-Pereleshin formula, a random encounter model. Our findings reveal a declining trend among herbivores, while no significant changes were detected in carnivores over the study period. Cattleposts showed negative associations with most species, while burned areas were positively associated with herbivore densities but generally negatively associated with carnivores. Vegetation characteristics and the distribution of mineral pans were also often associated with species density. Despite growing pressures, the northern WKCC continues to support wildlife and enable movement — albeit less than in the past— especially in areas distant from human activity. To safeguard its ecological function, we recommend integrated land-use planning that protects key habitats and corridors while promoting nature-based livelihoods. Involving local communities in research and conservation is essential. In the Kalahari — as globally— where tracking substrates and Indigenous knowledge coexist, track-based monitoring offer cultural and economic benefits that can foster human-wildlife coexistence, uphold land rights and support community-led resource management.

Keywords: Track survey; Animal indirect signs; Wildlife abundance; Formozov–Malyshv–Pereleshin formula; Community-based conservation; sdmTMB

I. Introduction

The quality and availability of essential resources for both humans and non-humans depend entirely on ecosystems health and balance. Yet, of the estimated 8 million animal and plant species living on the planet, around 1 million are believed to be threatened with extinction, reflecting various levels of ecosystem dysfunction (IPBES, 2019). To mitigate biodiversity loss, ‘modern’ biological conservation primarily relies on a network of Protected Areas (PAs) and Other Effective Area-Based Conservation Measures (OECMs), 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 Parties (COP15) in late 2022 under the Convention on Biological Diversity (CBD). However, an additional but largely undocumented number of territories and areas 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 protection. It also hosts the highest proportion of countries with Indigenous Peoples (Garnett et al., 2018). This is encouraging for further conservation efforts, as the continent harbours exceptional biodiversity, including over a quarter of the planet’s mammal species (IPBES, 2018), along with some of the world’s most iconic species that often serve as flagship species for conservation.

The semi-arid Kalahari Desert (hereafter referred as the Kalahari), spanning Botswana, Namibia, and South Africa, is one such region, harbouring remarkable biodiversity and 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 extensive, connected habitats to access key resources and ensure long-term survival (CI, 2010a; Keeping et al., 2022b; Perkins, 2019; Verlinden, 1998). In Botswana, the Kalahari spans two-thirds of the country (**Figure 5-1 – Southern Africa**), including the country’s largest Protected Areas (PAs) —Central Kalahari Game Reserve (CKGR) and Kgalagadi Transfrontier Park (KTP). These PAs are connected by Wildlife Management Areas (WMAs), forming the extensive “Western Kgalagadi Conservation Corridor” (WKCC), which supports wildlife movement and access to key resources between adjacent livestock farming areas (CI, 2010a) (**Figure 5-1 - Botswana**). This landscape is possibly one of the largest remaining unfenced wilderness areas in sub-Saharan Africa (WCS & CIESIN, 2005). The WKCC WMAs host small villages, each allocated a 20-km development zone for exclusive use (Ministry of Local Government, 2009) (**Figure 5-1 – Study area**). Within these zones and in adjacent livestock

farming areas, cattleposts — free-ranging livestock systems centred around water points supplied by pumped underground water (Perkins, 1996)— have been prioritised over wildlife-based livelihoods. In the absence of fences, livestock regularly encroaches in WMAs (Van der Weyde, 2019; pers. obs.). Even livestock from fenced farms bordering some WMAs occasionally graze unlawfully within them due to poor fence maintenance (pers. obs.).

Despite recommendations for stronger protection of key WKCC WMAs and a comprehensive management plan, progress has been slow. As a result, they face ongoing anthropogenic encroachment, creating complex challenges for wildlife conservation, human-wildlife coexistence, and socio-economic development, further exacerbated by climate change. On the ground, wildlife conservation efforts need spatial and temporal insights into species population size, factors affecting populations, habitat suitability, and connectivity across landscapes, among others. In this context, systematic wildlife monitoring across large areas is essential to track population trends and adapt conservation strategies. Aerial surveys, traditionally used by the Botswana Government, have become increasingly infrequent and financially demanding. Alternatively, the region's sandy terrain and the presence of traditional Indigenous tracking skills provide an ideal setting to study animals through their tracks (i.e. footprints). In particular, the Formozov-Malyshev-Pereleshin (FMP) formula is the most recent track-based method applied in the Kalahari, showing promising results for estimating absolute wildlife densities (Ahlsweide et al., 2019; Gielen et al., 2024; Keeping, Burger, et al., 2018). Additionally, animal track surveys conducted between 2008 and 2018 enabled a comprehensive modelling of wildlife occupancy and landscape connectivity across the WKCC (Keeping et al., 2022a, 2022b), providing the foundation for an Integrated Land Use Management Plan (ILUMP) (Tshukudu, 2024) awaiting implementation. This ILUMP proposes practical, sustainable land-use strategies to guide policy, informed by environmental science and socio-economic realities. Meanwhile, anthropogenic development continues to expand, highlighting the need for follow-up research - ideally at a finer scale and incorporating local Indigenous knowledge. Larger species are a key focus in the region due to their ecological importance, space requirements, umbrella effect, tourism value, and vulnerability to disturbance (Lindsey, Alexander, et al., 2007; Malhi et al., 2016; Ripple et al., 2014; Ripple et al., 2015).

Various factors likely influence the abundance, distribution and movements of large wildlife and can be roughly grouped into ecological and anthropogenic variables. In the semi-arid Kalahari, ecological variables like

rainfall are seasonal and often localised, dramatically affecting vegetation productivity on which large herbivores depend (van Rooyen & van Rooyen, 1998). In turn, large carnivores, though somewhat opportunistic, rely on prey availability (Mills, 1984). Species may favour denser or more open vegetation cover depending on their foraging strategies or anti-predator adaptations (Bothma & Walker, 1999; Smithers, 1971). Pans and dry fossil valleys, characteristic of the Kalahari, provide critical resources. Pans are isolated clay depressions that hold ephemeral water after rainfall (Lancaster, 1974). Both provide nutrient-rich vegetation and mineral licks, particularly valuable for grazers and during the calving season (CI, 2010a; Parris & Child, 1973). Wildfires, mostly human-induced, occur annually in the dry season, triggering green vegetation flushes with the first rains of the wet season (Maabong & Mphale, 2021; Skarpe, 1980), usually attractive to herbivores (Ngwamotsoko, 1985; Verlinden, 1997). Anthropogenic variables primarily revolve around settlements and livestock farming. Cattleposts, and to a lesser extent fenced farms, are catalysts for human-wildlife conflict (Karunya Consulting et al., 2020; Klein, 2013), cause wildlife habitat loss and land degradation within WMAs (Cooke, 1985; Parris & Child, 1973; Verlinden et al., 1998), and may serve as stepping stones for 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).

The ongoing proliferation of cattleposts and the imminent conversion of WMA portions to farming in parts of the WKCC threaten its functionality as wildlife habitat and movement corridor. Further, such negative impacts impede the development of natural resource-based livelihoods. Therefore, this study aims to provide updated, fine-scale insights into the northern part of the WKCC with three main objectives: (1) estimate *absolute* population densities of 12 large and one medium-size wildlife species (hereafter collectively referred to as 'large'), (2) identify key predictors of species' *relative* density (using relative track densities as proxies), and (3) derive predictive maps across the entire study area to highlight areas with higher relative density of wildlife and potential movement pathways. Leveraging both Indigenous knowledge and modern technology, we conducted biannual track surveys along linear transects from 2019 to 2021, within WMAs of the Ghanzi District. First, we calculated wildlife population densities over time to assess the status of 12 large and one medium-size wildlife species (hereafter collectively referred to as 'large'). Next, we analysed how species track densities within 4km² grid cells intersected by transects are affected by

environmental variables. Findings were used to model the remaining wildlife strongholds at both species and guild levels and to identify preferred movement pathways in this altered landscape. These results aim to inform conservation decisions and land-use planning to protect and sustainably develop this region. By demonstrating the versatile use of track data, we also seek to promote research methodologies that engage collaboration with local communities, both in the Kalahari and in other regions worldwide with suitable tracking substrates.

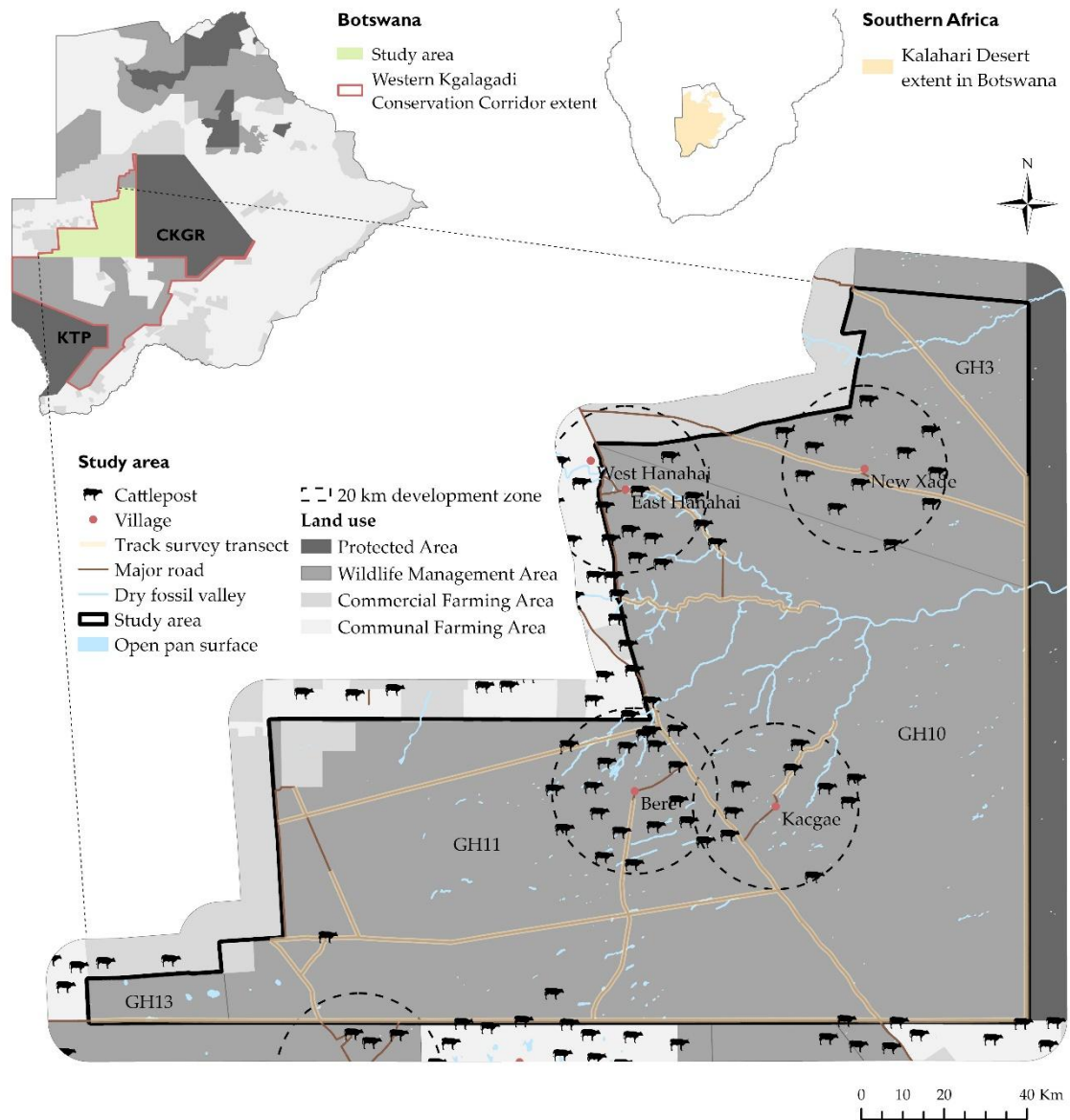


Figure 5-1 Location of the study area and its landscape features within the Western Kgalagadi Conservation Corridor (WKCC). Together with the Central Kalahari Game Reserve (CKGR) and Kgalagadi Transfrontier Park (KTP), the WKCC forms an extensive free-ranging wilderness within Kalahari Desert of Botswana, one of the largest of Sub-Saharan Africa.

2. Materials and Methods

2.1. Study area

Botswana land use is divided among partly unfenced PAs, unfenced Wildlife Management Areas (WMAs), fenced Commercial Farming Areas (CFAs) with enclosed farms, and unfenced Communal Grazing Areas (CGAs) 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 due to relatively lower anthropogenic pressure (DWNP, 2015, 2018).

We surveyed four WMAs in Ghanzi District, Botswana: GH10, GH11, GH13 and the southern part of GH3 (**Figure 5-1 – Study area**). Together, they span approximately 22,000 km² between 21.7°–23.3°S and 020.6°–022.8°E, forming the northern section of the WKCC (**Figure 5-1 - Botswana**). The sandy ground supports grasses, shrubs and scattered trees forming a more or less open savannah 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; DHV, 1980; DMS, 2021). Natural surface water is ephemeral, found only in pans or parts of fossil valleys after rainfall (Lancaster, 1974), both of which are present throughout the region. The study area also includes four villages and 97 cattleposts (as of the study period) within their development zones, plus a 10 km CGA buffer around the study area's perimeter. Roads are sparse, mostly sand tracks with low traffic, except for a single tarred road marking the boundary between GH10 and GH11.

2.2. Species data collection

Track surveys were conducted biannually for three years (2019-2021), in May (June in 2020 due to COVID restrictions) and November, to collect track data on 13 of the largest Kalahari herbivores and carnivores: eland (*Taurotragus oryx*), gemsbok (*Oryx gazella*), red hartebeest (*Alcephalus caama*), greater kudu (*Tragelaphus strepsiceros*), blue wildebeest (*Connochaetes taurinus*), ostrich (*Struthio camelus*), springbok (*Antidorcas marsupialis*), African wild dog (*Lycaon pictus*), brown hyaena (*Hyaena brunnea*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), lion (*Panthera leo*), and spotted hyaena (*Crocuta crocuta*). May and November mark the transition between the dry and wet seasons, avoiding 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 towards 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 to detect wildlife moving through the landscape.

Each survey sampled the same 1,037km of transects over an average of 24 days (including logistic breaks), starting from the north-east of the study area (GH3-GH10) and ending in its western part (GH11-GH13) (**Figure 5-1 – Study area**). Transects covered nearly all major existing 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 sample gradients of environmental variables, as well as intercept historical movement routes of wildlife. The data collection team consisted of a single vehicle driven by a recorder, and a pair of Indigenous certified trackers (Tracker III or Master Tracker, CyberTracker Conservation's Tracker Certification System (Liebenberg et al., 2018)) who sat in front of the bonnet as observers. Two pairs of trackers assisted with the surveys: one pair primarily covering GH3-GH10 and the other focusing mostly on GH11-GH13. The personnel remained unchanged, except for the recorder in May 2021 and one tracker who regrettably passed away before the 2021 surveys. This has no consequence for data interpretation as differences in track detection probabilities between tracking teams have been shown to be minimal (Gielen et al., 2024). Driving speed was capped at 10 km h⁻¹ 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 and time, species, number of individuals, track age class (i.e. ≤24h, 2 days, 3 days, 3 days +, 1 week +, 1 month +) and GPS location (see **Appendix 5A** for a description of our CyberTracker application).

2.3. Data analysis

2.3.1. Absolute population density estimates

The sampling and analysis protocol adhered to the Formozov-Malyshev-Pereleshin (FMP) formula approach, with further details provided in Gielen et al. (2024). Estimating the absolute population density ($\hat{D}$) for the study area via the FMP formula implies correcting the estimated number of fresh (≤ 24 hours 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 hours ($\hat{M}$) within the study area:

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

One track interception represents the intersection between one individual animal's movement path and the survey transect, visible as one or a series of footprints on the transect (see **Figure 3-2** in Chapter 3). The probability that an animal movement path intersects with the total transect length at least once ($\hat{p}_1$) is inherently accounted for by all the FMP parameters, of which the accuracy of $\hat{M}$ is key (see **Appendix 4A** in Chapter 4). The probability of fresh track detection by observers ($\hat{p}_2$) 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 $\hat{x} = \frac{x}{\hat{p}_2}$. For brown hyena, x was not corrected, as $\hat{p}_2$ was estimated at 1 due to species' propensity to follow road features for extended distances, making them hard to miss (pers. obs.).

For each of the 13 species, the estimate of density 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 $\hat{M}$ collected in the Kalahari region were used for all species except springbok, for which data were insufficient to capture the species' full movement range. Instead, an allometric estimate based on the body mass-daily travel distance relationship in artiodactyls (see Carbone et al. (2005)) was used, further corrected with a factor of 1.917 to account for the greater daily travel distances observed in Kalahari herbivore species compared with those in the species used in the Carbone relationship (see Chapter 4). The uncertainty around the estimate was calculated in R (version 4.4.1) as bias corrected and accelerated

(BCa) 95% confidence intervals via non-parametric bootstrapping (see Keeping (2014)).

2.3.2. Relationship between relative track density and environmental predictors

a) Relative track density estimates

The study area was overlaid with a grid of 4 km² cells, with each cell's width approximately half the $\widehat{M}$ of springbok and a surface area approximating half its home range ($\sim \widehat{M}^2$ following the theory explained in Stephens et al. (2019)). As the least mobile of our focal species, this choice represents a good compromise between the need for enough grid cells with track detection and a fine enough resolution to produce spatial outputs that can inform land use planning recommendations.

In a low-density environment, the number of fresh (≤ 24 hours old) track interceptions is limited, potentially yielding a null $\widehat{D}$ for a large proportion of grid cells, especially for rare species. Including older tracks, e.g. tracks aged under a week old (i.e. ≤ 24 hours, 2 days, 3 days, and 3 days +), enables the utilisation of most of the collected data, likely increasing the number of grid cells with tracks present. Tracks older than a week could theoretically be included as well but linking them to temporally dynamic predictors becomes overly complicated, and there is an increased risk of species misidentification. However, because track disappear as they age and do so at an unknown rate, $\frac{\hat{x}}{s}$ can no longer be reliably linked to $\widehat{M}$. Therefore, when retaining older tracks in $\hat{x}$, the track index $\left(\frac{\hat{x}}{s}\right)$ must be used alone as a measure of relative track density calculated for each grid cell, serving as a proxy for relative animal abundance in place of $\widehat{D}$. This approach is valid at the species level, as $\widehat{M}$ (addressing $\hat{p}_1$) is assumed constant across spatial and temporal scales over which the FMP formula is used to compute animal density. Seasonal variations of $\widehat{M}$ are plausible but assumed smaller than the variation in track density sought to be detected for our focal species (see Chapter 4). Finally, $\hat{p}_2$ is sufficiently constant across observers, transect substrate type, and livestock disturbances in our study area (Gielen et al., 2024). Fresh tracks are more detectable than old tracks, but there is no evidence to support significant variation in detection rate among grid cells at species level (Gielen et al., 2024). In brief, where $\hat{p}_1$ and $\hat{p}_2$ are being controlled, the number of track interceptions (fresh + old) on the transects is proportional to the number of animals present, theoretically up to a distance $\widehat{M}$ around them.

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. For brown hyena, leopard, African wild dog, and cheetah datasets, track counts from grid cells with the highest track densities were reassigned to the nearest surveyed cells (2 km away) when recorded on very small transects, up to approximately 600 m (3, 3, 3 and 2 cases, respectively). This reduced model fit issues for such low-density species while retaining the data without introducing significant bias.

b) Environmental predictors

For all environmental predictors, we extracted their values in each grid cell for each survey (**Table 5-1**). Predictor raster layers were created in ArcGIS Desktop 10.8. (see **Appendix 5B** for detailed steps). The distance to landscape features was calculated from the grid cell centroids. Cumulative rainfall for May/June surveys was calculated as the total rainfall from the previous wet season (November to April). For November surveys, marking the start of the rainy season, each cell was assigned the cumulative rainfall recorded from October 1 (when isolated showers may begin) until the day before the cell was surveyed. Burned areas for the November surveys were created from the cumulative burned pixels from the previous dry season (May–October) and up to the day before the cell was surveyed. The same layer was used for the following May/June survey, as burn scars remain visible on satellite imagery even after the wet season re-growth. When grid cells overlapped multiple rainfall or burned data pixels — available at a different spatial resolution (see **Table 5-1**)— the maximum value was used (i.e. 1 for burned variable as binary). A vegetation cover map and survey-specific Modified Soil-Adjusted Vegetation Index (MSAVI (Qi et al., 1994)) maps were initially created from Sentinel-2 10 m resolution images in Google Earth Engine (see **Appendix 5C** and **Appendix 5D**). In ArcGIS, the percentage of grass, shrub, and large tree and shrub pixels was then extracted for each grid cell and its neighbouring cells — eight neighbours for herbivore models and 99 for carnivore models — as separate variables. Considering the mosaic nature of vegetation, this approach accounts for the animals' spatial awareness beyond a single grid cell, with diameters of approximately 6 km for herbivores and 20 km for carnivores, corresponding to the guilds' estimated average daily travel distances. The MSAVI map was simply resampled at the grid cell size resolution using the average pixel value. A relative prey density map for carnivore models was created by summing herbivore predicted relative track density layers, each weighted by the inverse of the species' estimated daily

travel distance as in the FMP equation. All continuous predictors were standardised using z-scores within each survey.

c) Modelling of relative track density

For each species, we modelled relative track density as a function of the fixed-effect environmental predictors using spatial geostatistical generalised linear mixed models via the sdmTMB package (R version 4.4.1) (Anderson et al., 2024). Spatially correlated random effects were incorporated through a triangulated mesh of vertices, approximating spatial variability of 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.

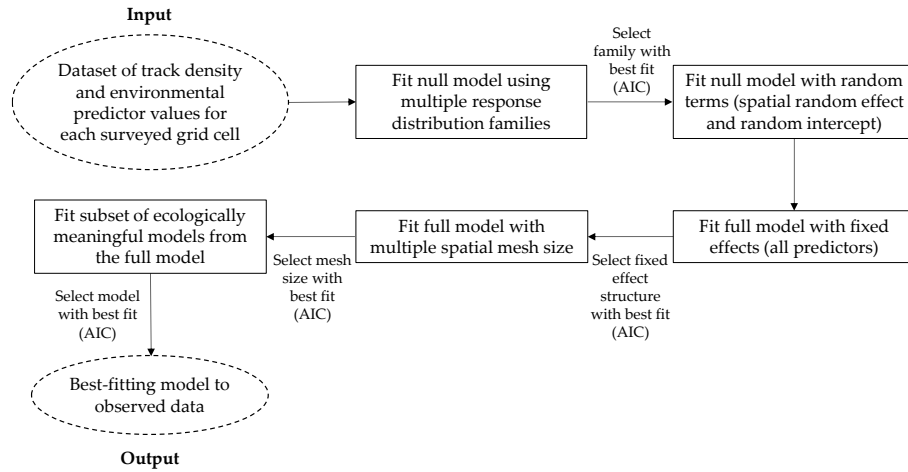


Figure 5-2 Overview of the workflow used to model observed relative track density as a function of environmental predictors using the sdmTMB R package and model selection based on AIC.

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 non-zero 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 structure 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), 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, along with the full model, using AIC to identify the best-fitting model to observed data. The coefficients of the predictors retained in the selected best model were examined to understand their respective influence on relative track density (see **Figure 5-2** for an overview of the entire workflow). If multiple models had a $\Delta\text{AIC} \leq 1$ compared with the best model, the one with the most predictors was selected to assess their impact on relative track density. If the number of predictors was equal, the model with the best AIC was retained. We chose this strategy to prioritise avoiding false negatives (i.e., missing a significant predictor) over false positives. Model diagnostics were conducted by visually inspecting randomised quantile residuals.

Table 5-1 Response variable and environmental predictors used to model relative track density. For temporally dynamic variables, labelled as "survey-specific" in the "Variable type" column, a spatial layer was created for each survey.

Variable type	Model component	Variable name	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", "Wild_Dog", etc.)	Number of individual track interceptions (≤ 24 h to 6 days old) per kilometre of transect.	0-82 km ⁻¹ (across all species)	NA	Six biannual track surveys (2019-2021) conducted along 1,037 km of transects in GH3/10/11/13 WMAs, Ghanzi District, Botswana
Predictor – continuous (survey specific)	Main 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 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 from Ngami Data Services (2009) supplemented by remote sensing
Predictor – continuous	Main effect	Distance to pan ("Dist_Pan")	Distance to closest edge of the closest pan	0-30 km	Negative relationship for herbivores, maybe indirectly for carnivores too	Remote sensing by Arthur Albertson Consulting (2024) and this study
Predictor – continuous	Main effect	Distance to major pan ("Dist_Pan50")	Distance to 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 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 effect	% Grass ("Grass_cove" for herbivores and "Grass_co_c" for carnivores)	Proportion of 10m grass pixels within a zone of 3x3 grid cells (the grid cell of interest and its 8 neighbouring cells) for herbivores, and a zone of 5x5 grid cells for carnivores .	0-87 % and 0-64%	Relationship depending on the species	Maximum likelihood supervised classification on Sentinel-2 10m imagery median values from Nov 2019 and June 2020.
Predictor – continuous	Main effect	% Shrub ("Shrub_cove" and "Shrub_co_c")	Idem as above, for shrub (~<2-3m).	0-90% and 0-84%	Idem as above	Idem as above

Predictor continuous	-	Main effect	fixed	% Large tree and shrub ("Tree_cover" and "Tree_cov_c")	Idem as above, for large tree and shrub (->2-3m).	0-55% and 0-37%	Idem as above	Idem as above
Predictor continuous (survey specific)	-	Main effect	fixed	Burned area ("Burned")	Binary variable indicating the grid cell as burned (1) or not (0) over the previous dry season for each November survey and their following May/June survey.	0, 1	Positive relationship as burned ground produces high quality vegetation during re-growth	MODIS MCD64A1 Burned Area Product 500m
Predictor continuous (survey specific)	-	Main effect	fixed	Modified Soil-Adjusted Vegetation Index ("MSAVI")	Index of vegetation density and health	-0.06-0.68 (across all surveys)	Positive relationship	MSAVI equation applied on Sentinel-2 10m imagery median values for each survey period
Predictor continuous (for large carnivores only)	-	Main effect	fixed	Relative track density of prey species ("Prey_densi")	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 1,037 km of transects in GH3/10/11/13 WMAs, Ghanzi District, Botswana
Predictor continuous (survey specific)	-	Main effect	fixed	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 (Mays/June) 0-82 mm (Novembers)	Positive relationship	TAMSAT 4km imagery (Maidment et al., 2014; Maidment et al., 2017; Tarnavsky et al., 2014)
Predictor categorical	-	Main effect	fixed	Region ("Region")	Regional separation of study area at the level of the tar road marking 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 – -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, Nov 2019, June 2020, Nov 2020, May 2021, Nov 2021		Six biannual track surveys (2019-2021) conducted along 1,037 km of transects in GH3/10/11/13 WMAs

2.3.3. 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()`), with folds based on spatial data clusters. Prior to this, we ensured that the selected mesh size for all models produced Matérn range of at least half the species' $\bar{M}$. While modelling small-scale variations in relative track density may improve statistical fit, it can create overly localised hotspots confined to the survey transects, which are not relevant for larger-scale inference. 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. For the Tweedie models or the positive component of the hurdle models, we used the mean absolute error (MAE), supplemented by a visual comparison of predicted versus observed relative track density values. Then, we applied model stacking (via `sdmTMB_stacking()`), optimizing normalised weights to maximise the total log-likelihood across models (Yuling et al., 2018). For models with weights > 0 , we generated relative track density predictions (via `predict()`) for unsurveyed grid cells using environmental data from those cells. Next, we calculated a weighted average of the predictions based on the stacking weight results to create a unified relative track density map. To quantify the uncertainty in the relative track density spatial predictions, we conducted 100 simulations from each model's joint precision matrix and applied the ensemble weighting to each draw. From these results, we derived the coefficient of variation for each grid cell.

As described in section 2.3.2 a), species-specific relative track density maps serve as a proxy for species relative density. Therefore, we generated overall carnivore and herbivore relative density maps by summing predicted track densities across species, weighted by the inverse of their respective $\bar{M}$ (like the FMP equation). This approach ensures that the relative abundance of each species is respected. To highlight areas of higher wildlife density across the landscape, two additional maps were created, showing carnivore and herbivore relative density values above the 20th and 40th percentiles, respectively. These percentile values were chosen based on the quasi-normal distribution of carnivore and Pareto-like distribution of herbivore relative density data.

Appendix 5E provides the R script for brown hyena, gemsbok and springbok as examples, with a detailed description of the steps for building

sdmTMB models, conducting model comparisons, performing cross-validation, and generating prediction outputs.

3. Results

We collected a total of 25,357 tracks across 14,450 locations for all 13 species combined. Of these, 9,577 fresh tracks were used for population density estimation, while 22,793 tracks up to six days old were included in the spatial analyses. The spatial grid comprised 7,765 cells of 4 km². On average, 597 cells were sampled per survey, resulting in a total of 3,852 data points for each species' spatial analysis.

3.1. Absolute population density estimates

Gemsbok was the most abundant species across the study area, followed by red hartebeest, greater kudu, and ostrich (**Figure 5-3**). Herbivores made up 97.25% of the total species abundance, compared with 2.75% for large carnivores. Species abundance differed between regions, with blue wildebeest, springbok and spotted hyena primarily recorded in GH11-GH13, and lion exclusively in GH3-GH10.

No significant changes in large carnivore density were detected over the study period (**Figure 5-4A**). All herbivore species tend to decline, with significant decreases in blue wildebeest and springbok, and marginally significant declines in red hartebeest and greater kudu (**Figure 5-4B**). **Table 5-2** provides regional average density and derived abundance estimates for the entire study period.

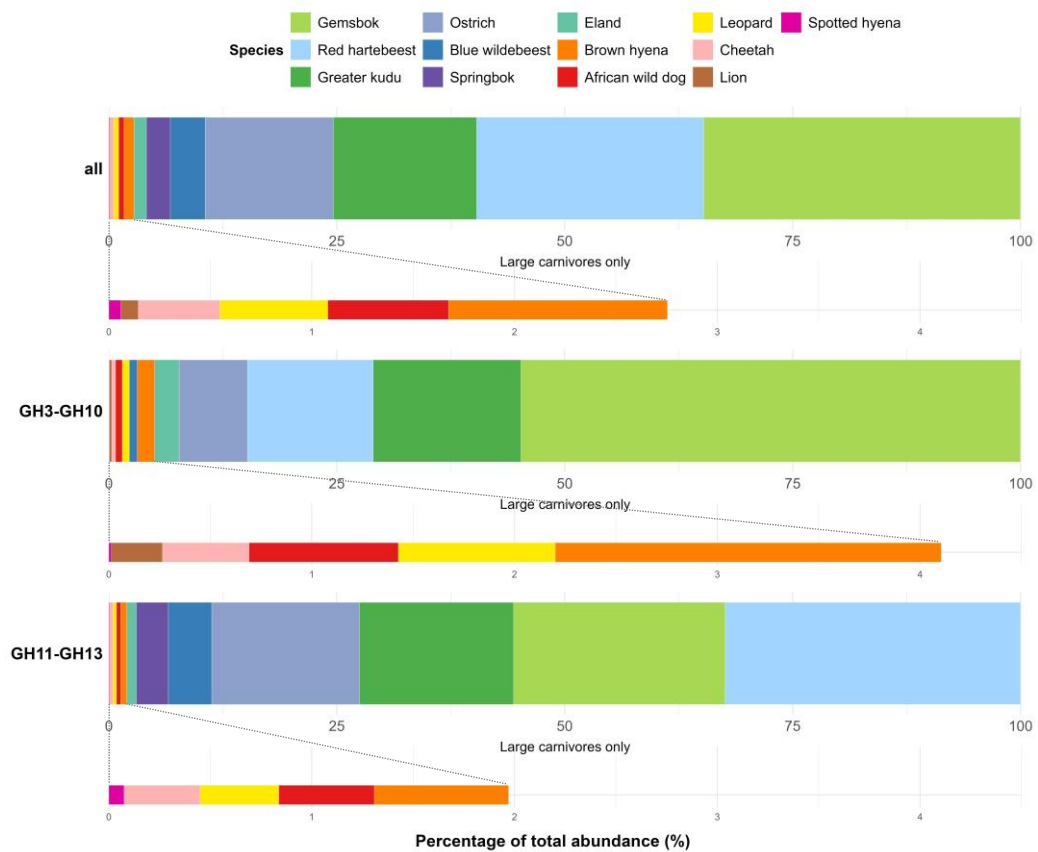
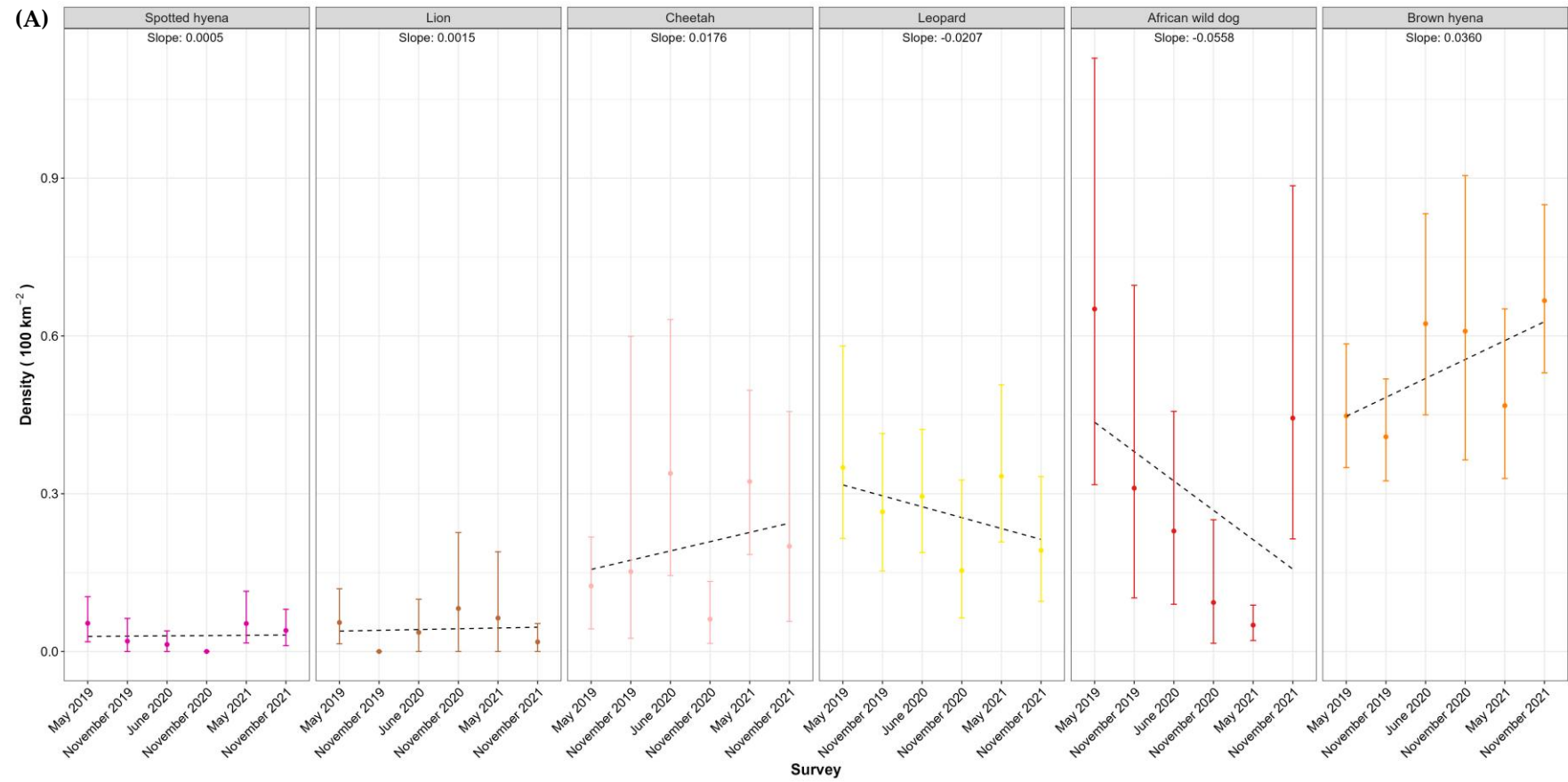


Figure 5-3 Percentages of total abundance for the 13 species studied, organised by region and displayed in ascending order of percentage. For each region, a zoomed-in view of the carnivore species is shown below the main bar plot.



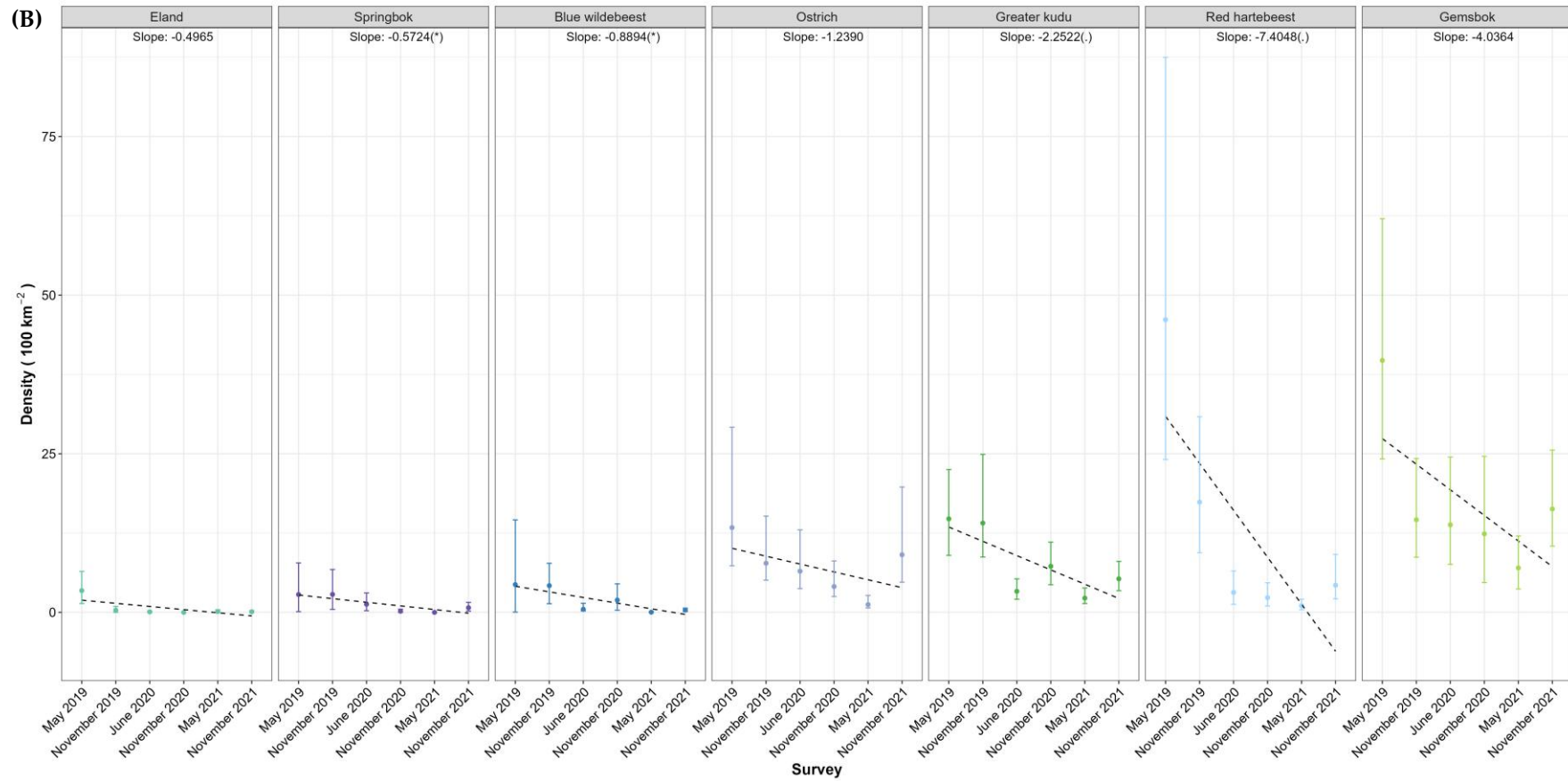


Figure 5-4 Population density estimates per survey per species for large carnivores (A) and large herbivores (B). Species-specific linear regression lines across surveys are shown as dashed lines, with slope coefficients provided. A “(.)” or “(*)” next to a slope indicates marginal significance ($p \leq 0.10$) or significance ($p \leq 0.05$) in its deviation from zero, respectively.

Table 5-2 Species-specific average density and derived abundance estimates per region across all surveys. The upper (UCL) and lower (LCL) confidence limits were calculated using bias-corrected and accelerated (BCa) 95% confidence intervals obtained through non-parametric bootstrapping.

Species	$\bar{M}$ (km)	Region	Density (100km ⁻²)	LCL BCa 95% (100km ⁻²)	UCL BCa 95% (100km ⁻²)	Abundan ce ^{a,b}	Abundan ce LCL BCa 95% ^a	Abundan ce UCL BCa 95% ^a
	$\pm$ SE (n)		^a	^a	^a			
African wild dog	24.60 $\pm$ 1.7 (12)	All	0.30	0.20	0.43	65	45	94
		GH3-GH10	0.25	0.15	0.41	32	19	52
		GH11-GH13	0.29	0.17	0.45	27	15	41
Brown hyena	31.10 $\pm$ 2.1 (42)	All	0.54	0.46	0.66	118	100	144
		GH3-GH10	0.65	0.54	0.80	83	69	102
		GH11-GH13	0.41	0.34	0.51	37	31	47
Cheetah	11.44 $\pm$ 0.15 (219)	All	0.20	0.14	0.29	44	30	64
		GH3-GH10	0.15	0.08	0.29	19	10	36
		GH11-GH13	0.23	0.15	0.34	21	13	31
Leopard	13.74 $\pm$ 0.81 (16)	All	0.26	0.21	0.34	58	47	75
		GH3-GH10	0.26	0.20	0.35	34	25	44
		GH11-GH13	0.24	0.17	0.32	22	16	30
Lion	19.4 $\pm$ 1.4 (16)	All	0.04	0.02	0.07	9	5	16
		GH3-GH10	0.09	0.04	0.14	11	6	18
		GH11-GH13	0.00	0.00	0.00	0	0	0
Spotted hyena	26.50 $\pm$ 1.7 (140)	All	0.03	0.02	0.05	7	4	10
		GH3-GH10	0.00	0.00	0.01	1	0	2
		GH11-GH13	0.05	0.03	0.07	4	2	7
Blue wildebeest	7.09 $\pm$ 0.12 (9)	All	1.90	0.97	3.75	416	213	820
		GH3-GH10	0.30	0.03	0.95	38	4	122
		GH11-GH13	2.93	1.38	5.90	267	126	539
Eland	10.47 $\pm$ 1.40 (12)	All	0.68	0.33	1.22	149	72	266
		GH3-GH10	0.92	0.37	1.70	117	47	217
		GH11-GH13	0.64	0.23	1.24	59	21	114
Gemsbok	5.60 $\pm$ 0.58 (17)	All	17.30	13.10	23.61	3786	2866	5165
		GH3-GH10	18.68	12.72	27.08	2381	1622	3453
		GH11-GH13	14.29	10.45	20.48	1305	954	1870
Greater kudu	5.84 $\pm$ 0.71 (18)	All	7.82	6.05	10.64	1712	1323	2328
		GH3-GH10	5.52	3.47	8.56	704	442	1091
		GH11-GH13	10.40	7.98	14.17	950	729	1294
Ostrich		All	7.00	4.90	13.11	1531	1073	2869

	5.16 ± 1.25 (5)	GH3-GH10	2.56	1.68	5.21	326	214	664
		GH11-GH13	9.98	6.99	18.63	911	638	1702
		All	12.39	8.02	21.10	2710	1754	4616
Red	5.84 ±	GH3-GH10	4.70	1.86	9.64	599	238	1229
hartebeest	0.91 (13)	GH11-GH13	19.94	13.61	32.77	1821	1243	2993
		All	1.31	0.61	2.46	286	134	538
Springbok	4.42 ^c	GH3-GH10	0.02	0.00	0.10	2	0	13
		GH11-GH13	2.17	1.02	4.01	198	93	366

^aThe values for GH3-GH10 and GH11-GH13 do not sum exactly to the total for the whole study area (“all”) because the 98 km boundary transect between GH10 and GH11 was included in the calculations for both GH3-GH10 and GH11-GH13.

^bAbundance calculations are based on areas of 21,881 km² for the whole study area, 12,748 km² for GH3-GH10, and 9,133 km² for GH11-GH13.

^cAllometric $\bar{M}$ corrected for Kalahari herbivore species, calculated with a body mass of 38kg (Kingdon, 1997), following the artiodactyls rule of Carbone et al. (2005) (n=22).

3.2. Relationship between relative track density and environmental predictors

Below, illustrated by **Figure 5-5**, we present the “best” relative track density model for each species, selected as per section 2.3.2 c). Track density is also interpreted as a direct proxy of relative animal density as explained in section 2.3.2 c). Where relevant, results are supplemented with insights from nearly equivalent models ($\Delta AIC \leq 1$), referred as “alternative models”. Grass and shrub cover percentages, being strongly inversely correlated ($r = -0.86$ for herbivores, $r = -0.87$ for carnivores), were never included together in a model. This means that a positive relationship with grass cover can be interpreted as a negative relationship with shrub cover, and vice versa. Finally, MSAVI represent green cover open to interpretation both in terms of vegetation health and total cover (Chen & Gillieson, 2009; Purevdorj et al., 1998; Qi et al., 1994). We present and discuss below the results species by species.

Gemsbok

Gemsboks were primarily negatively associated with cattleposts and, to a lesser extent, with fenced farms. They were more frequently present in the western part of the study area (GH11-GH13) and in unburned areas. Additionally, they appeared to be positively associated with areas with higher vegetation productivity, although showing no clear association with grassy or shrubby cover, and their density increased in regions with higher cumulative rainfall. These findings align with previous studies describing gemsbok as one of the most arid-adapted antelope species (DHV, 1980;

Pienaar, 1974), highly sensitive to human disturbance (Bergström & Skarpe, 1999; Verlinden et al., 1998), and with versatile habitat use influenced by local and seasonal conditions (Lehmann et al., 2020; van der Walt et al., 1984). Their narrow mouths allow them to selectively graze green grass leaves, even in tall, drier grasslands, and effectively browse from trees and shrubs (Knight, 1991). Regions with higher rainfall support greener vegetation and a greater abundance of water-storing tubers and melons, which are sought by gemsbok, particularly during the dry season to meet their moisture requirements (Eloff, 1984; van der Walt et al., 1984).

Greater kudu

Greater kudus, like gemsbok, were more prevalent in GH11-GH13 and unburned areas. Their presence was positively associated with regions with higher vegetation productivity, likely partly driven by their preference for woody canopy cover, as supported by their observed positive association with areas with large shrubs and trees cover. These provide forage, shade during hot summer days, insulation during cold winter nights, and camouflage from predator thanks to their particularly cryptic coat coloration (Berry et al., 2023; Butler, 2017; Fabricius, 1989). Although primarily browsers, kudus shift their diet during the wet season to include more grass (Butler, 2017; DHV, 1980), possibly linked to their density increase with grass cover. Daily habitat shift has also been reported, favouring open areas during the day and seeking more cover at night (Butler, 2017). Kudu presence also showed a weak positive association with the proximity to large pans, which would align with observed attendance at salt licks by Parris (1976). Kudu presence was negatively associated with the proximity to cattleposts, as also noted by Ngwamotsoko (1985), although weakly, while their density was positively associated with the proximity to fenced farms. Bush encroachment due to overgrazing are common around cattleposts and farms (Dougill et al., 2016; Skarpe, 1986), potentially creating an attractive habitat for kudu, which can easily jump over farm fences (Van der Weyde et al., 2021). However, human deterrence at cattlepost may partially offset this benefit. The lower kudu density near fossil valleys may reflect their prevalence in GH11-GH13, where such features are scarce. Yet, fewer tracks were observed in the Okwa valley (GH10). Lastly, kudu presence appeared positively associated with areas with lower cumulative rainfall, particularly in burned regions. This may reflect the overall decrease of rainfall from north-east to south-west in the study area, rather than a true positive association, which would be likely directed toward burned areas instead (Butler, 2017).

Red hartebeest

Red hartebeest showed a clear positive association with burned areas, especially those that had received higher rainfall. As predominantly grazers and more water-dependent than gemsbok, they benefit from the short green grass regrowth after fires (Ngwamotsoko, 1985; van der Walt et al., 1984; Verlinden, 1997). In this regard, alternative models also revealed a positive association between density and grass cover (e.g. $\beta_1 = 0.11 \pm 0.06$ (SE)). Similarly, our model indicated higher density in areas with less large tree and shrub cover. However, hartebeest presence appeared slightly higher in areas with large trees and shrubs, likely due to their shade-seeking behavior and activity reduction as a primary cooling strategy to cope with heat (DHV, 1980). The apparent ambivalence of this predictor aligns with Kok (1975) observations in DHV (1980), which describe red hartebeests as frequently found in transitional zones between structurally diverse plant communities, such as patches of woody savanna and grassland. Hartebeests were also positively associated with the proximity to major pans, where they have been reported to regularly exploit soil licks (Bergström & Skarpe, 1999; Parris, 1976; van der Walt et al., 1984), as supported by our results. They have also been observed to use pans at night (Silberbauer, 1965), possibly to enhance predator detection and facilitate escape. Lastly, hartebeests were negatively associated with the proximity to cattleposts as found in other studies, although they were more tolerant of them than gemsbok (DHV, 1980; Ngwamotsoko, 1985).

Ostrich

Ostriches were clearly more prevalent in GH11-GH13 compared with the GH3-GH10 region. Their slight negative association with the proximity to fossil valleys likely reflects pronounced regional distribution differences rather than a specific ecological preference, as numerous tracks were recorded in the Okwa valley (GH10). Ostriches are opportunistic mixed feeders and omnivores, well adapted to arid conditions (Milton et al., 1994). The slight positive association of their presence with grass cover and areas with higher vegetation productivity, as shown by our model, aligns with previous studies (Milton et al., 1994; Verlinden & Masogo, 1997). However, the effect is weak, suggesting a broad use of various habitat types and food sources (Milton et al., 1994; van der Walt et al., 1984). Our results also indicated a positive association with the proximity to pans, consistent with findings by DHV (1980) and Bergström and Skarpe (1999), where ostriches ingest mineral soil (Parris, 1976) and engage in sand bathing (pers. obs.). Lastly, although ostrich presence was negatively associated with the proximity to cattleposts, the wide

confidence interval overlapping zero around the point estimate suggests possible tolerance of cattleposts. As such, other studies have noted co-existence with livestock (Verlinden, 1997), arguing ostriches may benefit from maggots and beetles associated with cow dung (DHV, 1980).

Blue wildebeest

Blue wildebeest were primarily concentrated in the southern half of the GH11-GH13 region. In GH3-GH10, detections were limited to isolated occurrences in the Okwa valley and tracks near a farm of the Ghanzi block, which hold captive individuals. The apparent positive association between wildebeest density and proximity to fenced farms in our model likely reflects the latter, and the high density observed in the pan-rich habitats near Ncojane ranches, rather than a preference for the farms themselves. Similar to red hartebeest, blue wildebeest are grazers, even more strictly so. Accordingly, our model showed a positive association between their density and the proximity to pans and fossil valleys, which provide short grasses more easily grazed with their larger mouths (Knight, 1991). These habitats are also valuable for mineral licks, predator detection, and access to water following rains, as wildebeest are the most water-dependent of all Kalahari large herbivores (DHV, 1980; Parris, 1976; Selebatso, Bennitt, et al., 2018). In the same vein, the observed higher density in burned areas is consistent with their attraction to green grass flush after rains (Pienaar, 1974). The slightly higher presence in areas with more large trees and shrubs aligns with their cooling strategy (shade-seeking), a trait they share with red hartebeest (DHV, 1980; Selebatso et al., 2017). Blue wildebeest presence was negatively associated with MSAVI potentially reflecting their regional distribution, as the southwest of the study area typically receives less rainfall than the northeast (DMS, 2021). To a lesser extent, it may also indicate a preference for more open habitats (Smithers, 1971) or burned scars, which are expected to exhibit lower MSAVI signatures, at least in the dry season. Lastly, blue wildebeest were negatively associated with the proximity to cattleposts, although exhibiting a tolerance level comparable to red hartebeest (Verlinden, 1997).

Eland

Eland presence was strongly negatively associated with the proximity to cattleposts, as reported by other studies (Ngwamotsoko, 1985; Verlinden, 1997). They are mixed feeders, leaning more toward browsing than gemsboks, and can utilise a wide range of habitats. However, they are often found in open plains bordering woodlands with greater grass cover (DHV, 1980; Fabricius, 1989), consistent with our results. Furthermore, well adapted to

arid conditions, elands rely less on shade for heat mitigation (Fabricius, 1989). Like gemsboks, our model showed their density was positively associated with areas of higher vegetation productivity; they tend to target fresh green grass during the wet season and rely on browse and water-bearing plant organs during the dry season to fulfil their nutritional and moisture requirements (DHV, 1980; Smithers, 1971; Verlinden, 1997). Unlike other herbivores, we found that eland density was slightly negatively associated with the proximity to pans, as noted by DHV (1980) who observed them mostly in the sandveld. Van der Walt et al. (1984) also found no attractions to pans. However, Parris (1976) reported that elands do visit pans for mineral licks, though they likely spend less time near them compared with other herbivores. Lastly, elands are less common in areas with higher cumulative rainfall. Lastly, eland density was slightly negatively associated with higher cumulative rainfall. This may be due to their confinement —influenced by factors such as an avoidance of cattleposts— to a restricted portion of the study area, which coincidentally received less rainfall on average.

Springbok

Like blue wildebeests, springboks were almost exclusively found in the GH11-GH13 region, with one detection in the Okwa valley (GH10). Springboks are true mixed feeders, drawn to short grass and dwarf shrubs (Bigalke, 1972; Verlinden, 1997). They graze predominantly during the wet season on fresh green grass and rely on browse otherwise (Bigalke, 1972; DHV, 1980). This may explain the slight negative association between springbok density and grass cover and, consequently, the positive association with shrub cover (as the two are inversely correlated). Springbok presence was also more strongly associated with burned areas and higher rainfall, which promote the growth of green forage they seek (Bergström & Skarpe, 1999; Bigalke, 1972; Bonifica, 1992). However, springbok density was higher in unburned areas, reflecting an ambivalent relationship likely depending on the availability of green flush (see Van der Walt (1984) vs Ngwamotsoko (1985) and Verlinden (1997)). As a species of particularly open habitats (Smithers, 1971), springboks appeared less abundant in areas with denser large shrub and tree cover. Rather than seeking shade, they rely more on their thermoregulating pelage and body orientation relative to the sun (Hofmeyr, 1985; Smithers, 1971). Surprisingly, pans and fossil valleys were not retained as predictors, despite their known importance to the species (Bergström & Skarpe, 1999; DHV, 1980; van der Walt et al., 1984). This is likely due to springbok concentration in a limited portion of the south-western part of GH11-GH13, where fossil valleys are absent. Despite the abundance of pans there, their absence around the many other pans in the study area diminishes

the overall association with this predictor. Lastly, springboks appeared comfortable near cattleposts, as observed in an alternative binomial model ($\beta_1 = -0.73 \pm 0.91$ (SE), $\Delta AIC = 0.55$) and by other authors (Ngwamotsoko, 1985; Verlinden, 1997). This is likely due to the proximity of cattleposts to pans in GH11-GH13 and the availability of browse and short grass in heavily grazed areas.

Brown hyena

In the Kalahari, brown hyenas primarily scavenge and opportunistically hunt small food items, resulting in a highly diverse diet. About a quarter of their diet consists of fruits like the Tsama melon (*Citrullus lanatus*) and Gemsbok cucumber (*Acanthosicyos naudianus*), which help meet their moisture needs (Mills, 1990; Owens & Owens, 1978). This may partly explain their positive association with areas with higher rainfall, where such resources are more abundant (Bonifica, 1992). They were also clearly negatively associated with burned areas, which may offer little benefit to scavengers when still bare. Brown hyenas are the most common large carnivore in the Kalahari, adapting to a wide range of habitats (Bothma & Walker, 1999; Smithers, 1971). However, we observed a slight positive association with areas with higher shrub cover. In this regard, they have been observed to use bushes or low-branching trees for resting during the day, storing food, or sometimes establishing their den (Bothma & Walker, 1999; Mills, 1990). Owens & Owens (1978) noted that the species forage in closer habitats in the dry season compared with the wet season. Interestingly, they seemed to be slightly negatively associated with large pans. While they have been observed foraging near pans and drinking water when available (Bothma & Walker, 1999; Parris, 1976), this may be linked to the presence of spotted hyenas, a dominant competitor (Bothma & Walker, 1999), around some clusters of large pans in GH11-GH13. Lastly, they were only mildly negatively associated with the proximity to cattleposts. As they rarely prey on livestock, they are less vulnerable to human persecution than other predators (Boast, 2014; Karunya Consulting et al., 2020)

Leopard

Leopard density was predominantly negatively associated with the proximity to cattleposts, likely due to their significant involvement in livestock-related conflicts in the study area, making them likely targets for retaliation by farmers (Karunya Consulting et al., 2020; Klein, 2013). Otherwise, leopards are able to occupy extremely diverse habitats (Bothma & Walker, 1999). Our model also indicated leopards were slightly negatively

associated with the proximity to pans. Although they may drink at pans when water is available (Bothma, 2005; Parris, 1976), their openness does not align with their stalking hunting strategy and they were found unsuitable as resting sites – instead, pan may serve a role in navigational and communication activities (O'Malley et al., unpublished data). Although weak, their negative association with the proximity to fossil valleys might reflect the challenges of modelling a generalist species, as leopards were notably present in areas like the Okwa valley. This could also apply to their observed negative association with MSAVI. Unless lower MSAVI here partially reflects more open habitats, at least in the dry season when bushes and trees are greener than grass. In this context, as with lions, O'Malley et al. (unpublished data) report leopard preferences for open shrubland in a comparable Kalahari region. Such habitat is also preferred by duiker (*Sylvicapra grimmia*) or steenbok (*Raphicerus campestris*) (Pienaar, 1974; Smithers, 1971), which are favoured prey of leopards (Bothma & Le Riche, 1984; Stander, 1994).

African wild dog

African wild dogs appeared more present in GH3-GH10 region, although the difference was moderate. They also showed a clear positive association with areas with less shrub cover, which is consistent with their opportunistic cursorial hunting strategy primarily based on sight (Bothma & Walker, 1999; Jordan et al., 2023). Additionally, their presence appeared slightly positively associated with areas with lower cumulative rainfall and farther from fossil valleys. While this has limited ecological meaning in the study area, it may potentially reflect competition with other large carnivores (Bothma & Walker, 1999). African wild dogs are highly mobile and extremely wide-ranging, both as a food acquisition strategy and to avoid inter-specific competition with apex predators (Jordan et al., 2023). Combined with their low density, this behaviour likely introduces greater randomness to track locations compared with less mobile and more specialised species, complicating modelling. This may also explain why neither a positive nor negative association with the proximity to cattleposts was observed in our best-fitting model (and alternative models), despite African wild dogs frequently being involved in livestock-related conflicts (Karunya Consulting et al., 2020; Klein, 2013).

Cheetah

Cheetahs were more prevalent in the GH11-GH13 region. As stalker-coursing hunters, they favor open woodland savannas that provide a balance of visibility and hunting cover, increasing hunting success, reducing kleptoparasitism, and improving cub survival rates (Bothma & Walker, 1999;

Mills et al., 2004). This aligns with the observed positive association with areas with larger tree and shrub cover. The importance of scent-marking trees as cheetah social hubs (Melzheimer et al., 2020; Van der Weyde et al., 2017) further support our results. Their strong negative association with burned areas is consistent with their need for minimum cover. The model also showed a slight positive association with areas with higher large prey density, likely reflecting the overlap of cheetah tracks with springbok tracks in GH11-GH13 (see **Figure 5-6** g and k), a favoured prey species in Botswana (Klein, 2007). Cheetah density's positive association with the proximity to fenced farms is likely partly linked to their prevalence in the pan-rich habitat of GH11-GH13 adjacent to Ncojane ranches. However, cheetah adapt well to farmlands, which offer reduced competition with larger predators (Van der Weyde et al., 2021), with higher cub survival rate (Bothma & Walker, 1999). Distance to cattleposts was not retained as a predictor in the best-fitting model. In GH11-GH13, cheetahs' likely attraction to springbok, which occurred near cattleposts, may have outweighed the potential risk of persecution. Moreover, the species seems less implicated in livestock-related conflicts than some other large predators (Karunya Consulting et al., 2020; Klein, 2013).

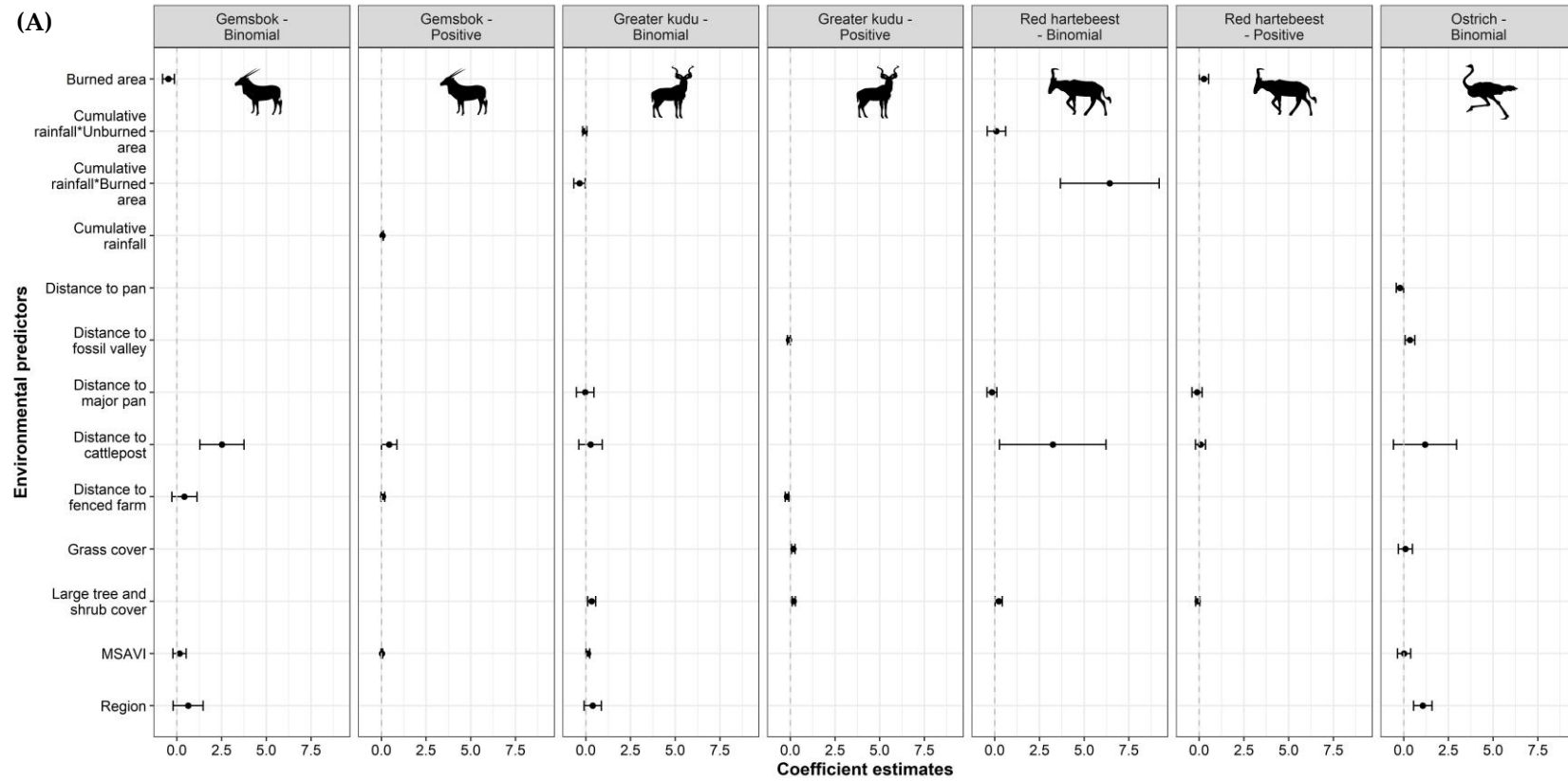
Lion

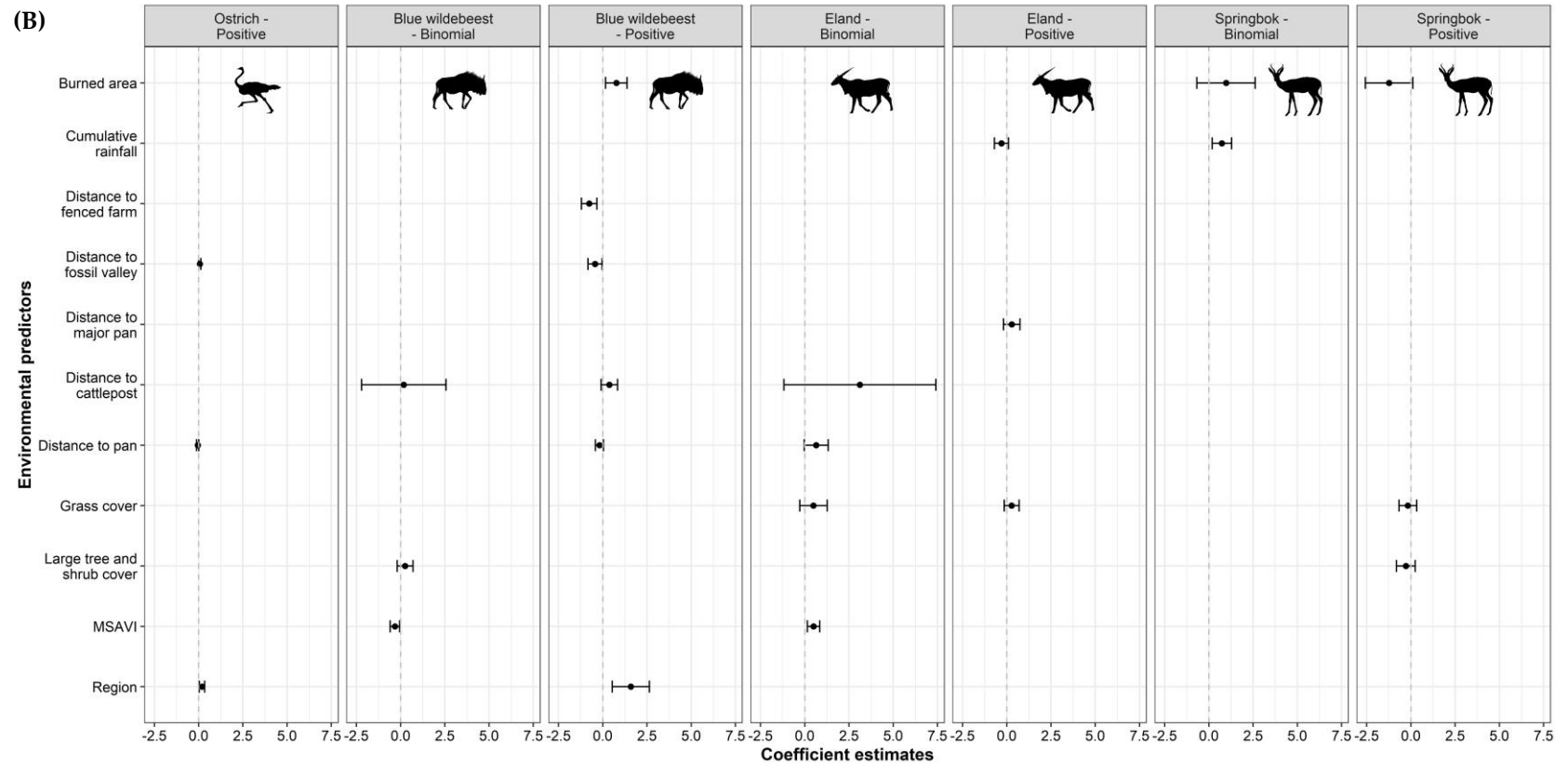
Lion presence was primarily negatively associated with the proximity to cattleposts. Their marked involvement in livestock-related conflicts seems to have contributed in their confinement to PAs and adjacent parts of WMAs (Bauer et al., 2014; Karunya Consulting et al., 2020). This is reflected in our data, where tracks were observed exclusively in GH3-GH10 on transects near the Central Kalahari Game Reserve (CKGR). Lion presence was also positively associated with large tree and shrub cover. Like for leopards, O'Malley et al. (unpublished data) reported a preference for open shrubland that facilitate stalking and ambush hunting tactics (Bothma & Walker, 1999). Taller trees and dense canopy cover were instead selected as resting sites. Therefore, the relatively high percentage of large tree and shrub cover modelled along the CKGR boundary transect, compared with the rest of the study area, may have introduced some bias. Lion density was also positively associated with unburned areas, consistent with their hunting strategy. However, its apparent weak positive association with areas with lower cumulative rainfall and those farther from fossil valleys lacks clear ecological meaning. The small sample size ($n = 44$) and restricted geographic scope of the positive model increased the risk of spurious effects. Similarly, the surprising lack of association with large prey density is likely due to lions being restricted to GH3-GH10, while the highest large prey densities occurred

in GH11-GH13, where lions were absent. Within GH3-GH10, predicted lion density closely overlapped with that of gemsbok and eland, two favored prey species in the region (**Figure 5-6** a, f and i) (Beukes et al., 2020; Stracquadanio et al., unpublished data).

Spotted hyena

Spotted hyaenas were primarily found in the GH11-GH13 region. Unlike brown hyaenas, they are less common in the Kalahari and tend to occur where large wild prey concentrations are higher (Bothma & Walker, 1999; Smithers, 1971; Van der Weyde et al., 2022). This aligns with their observed positive association with areas with higher large prey density, though with a great uncertainty in the estimated effect that may partly be caused by their small sample size, but could also reflect their adaptability. While primarily hunters, they also scavenge regularly to supplement their diet (Mills, 1990). Their negative association with the proximity to fossil valleys indicated by the model likely stemmed from valleys' scarcity in GH11-GH13, especially as Mills (1990) noted spotted hyena's affinity for dry riverbeds in the southern Kalahari. Conversely, spotted hyaena density was positively associated with the proximity to pans, which is unsurprising as pans attracted the large ungulates they prey upon (Parris, 1976), as confirmed in the above herbivore models. Furthermore, the openness of pans likely poses no issue for spotted hyenas, as they are cursorial endurance hunters (Bothma & Walker, 1999). Distance to cattleposts was not retained as a predictor in the selected best-fitting model. While spotted hyaenas occasionally prey on livestock, they appear to be less involved in human-wildlife conflict in the region compared with other large carnivores (Klein, 2013). However, the number of grid cells with a positive track density is particularly low for this species (n=32).





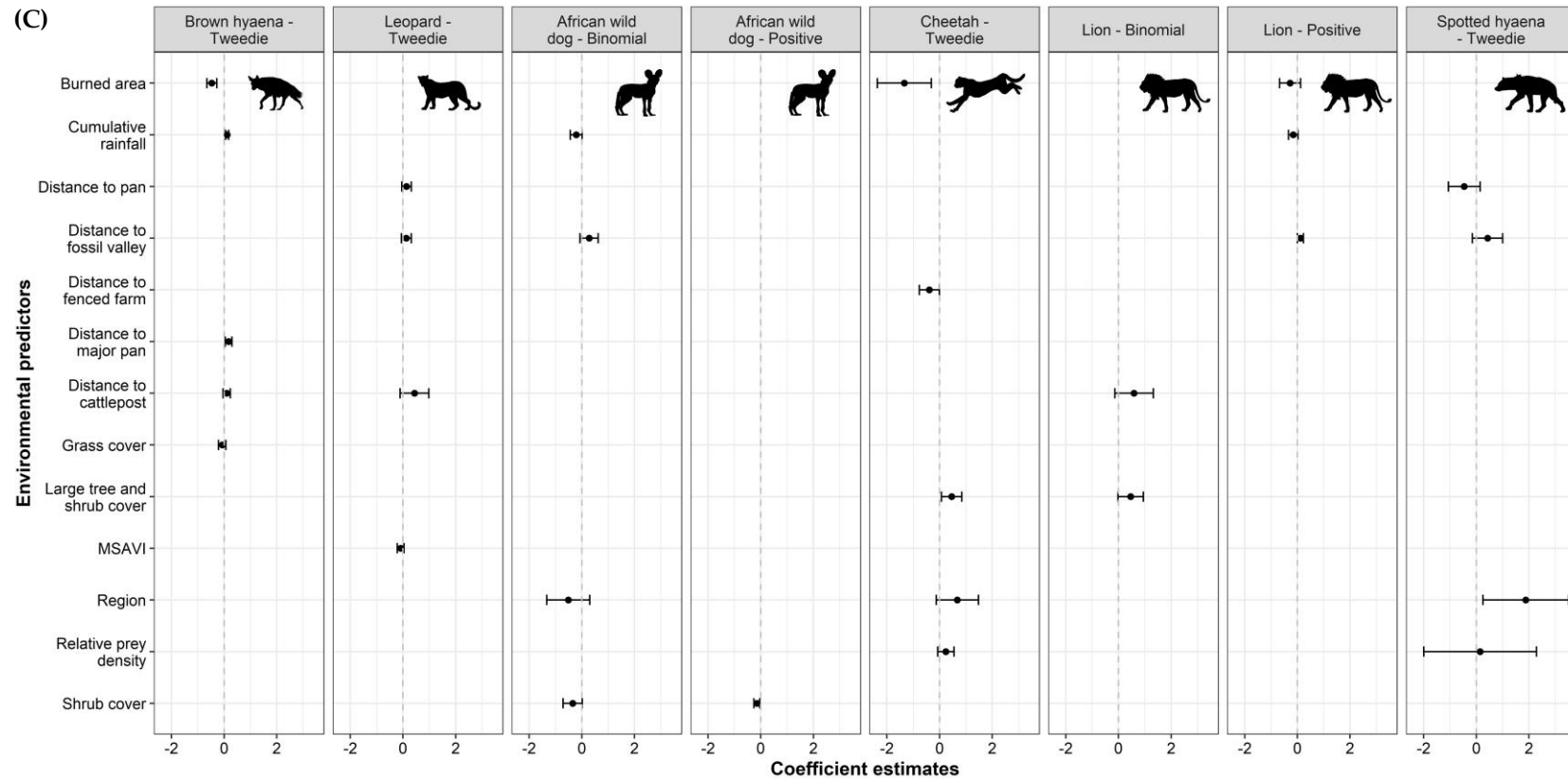


Figure 5-5 Coefficient estimates (on a log scale for positive and tweedie models, and log-odd scale for binomial models), along with their 95% confidence intervals, for the predictors included in the 'best' model selected to explain relative track density for each species.

(Panels (A) and (B) show results for herbivores, and Panel (C) for carnivores.

Icon sources: African wild dog, brown hyena, cheetah, leopard, spotted hyena from PhyloPic ([CC0 1.0](https://creativecommons.org/licenses/by/4.0/)). Greater kudu from PxHere Team ([CC0 1.0](https://creativecommons.org/licenses/by/4.0/)). 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 & Rob Slotow (vectorised by T. Michael Keesey) from PhyloPic ([CC BY 3.0](https://creativecommons.org/licenses/by/4.0/)). Lion by Gabriela Palomo-Munoz and blue wildebeest by Graham Montgomery from PhyloPic ([CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).

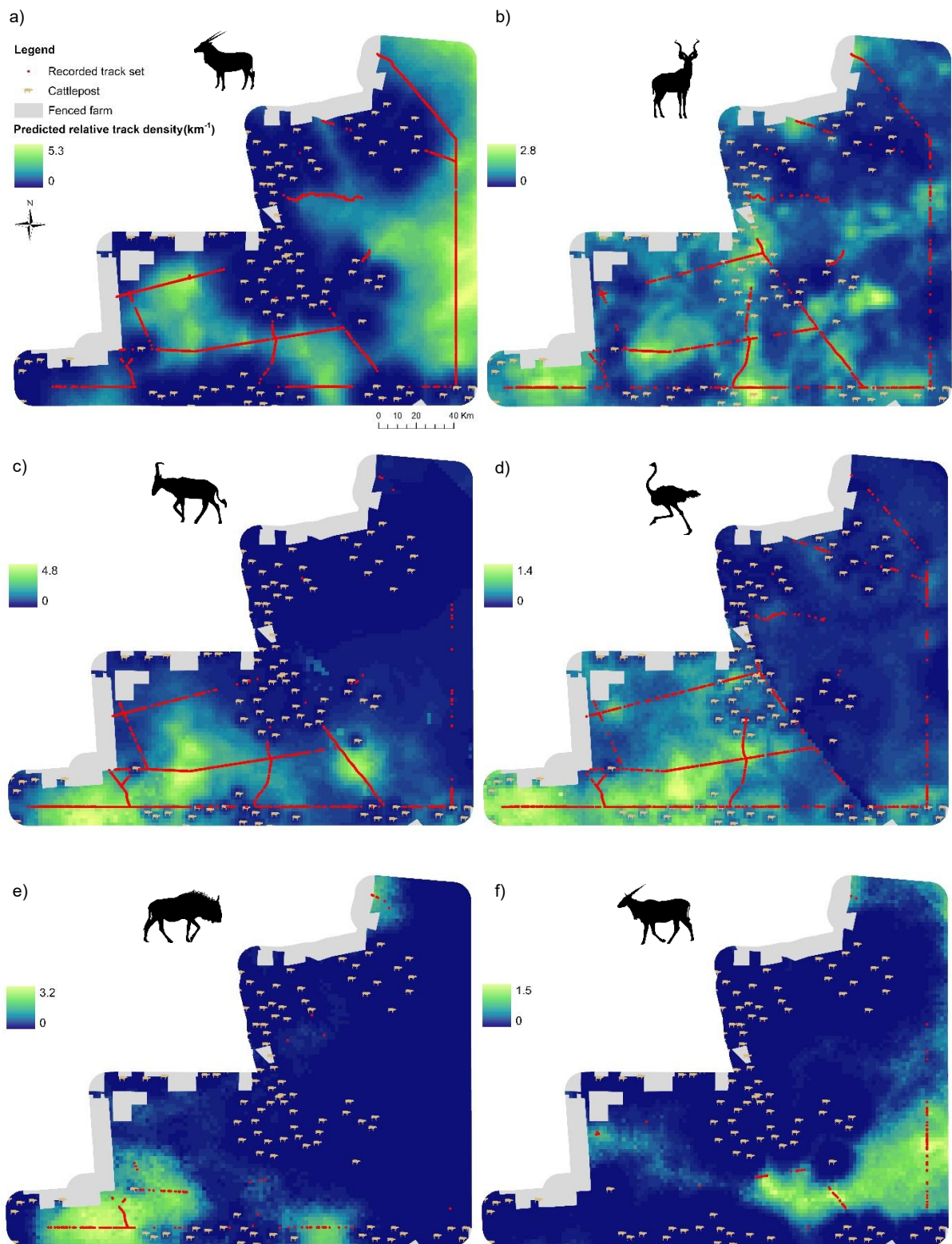
3.3. Prediction of relative wildlife density

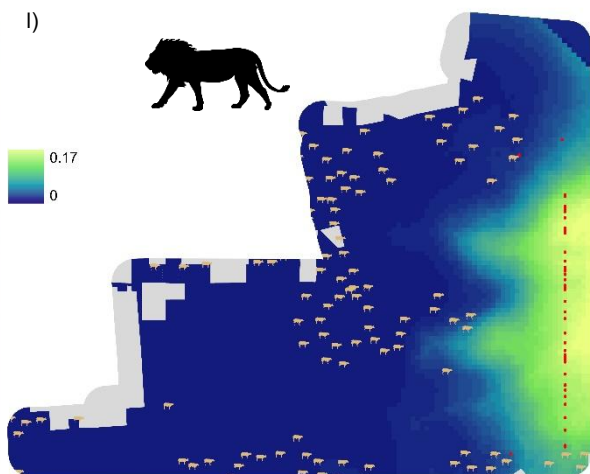
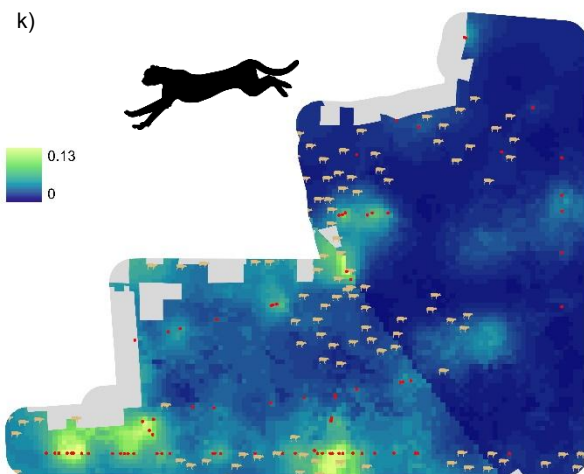
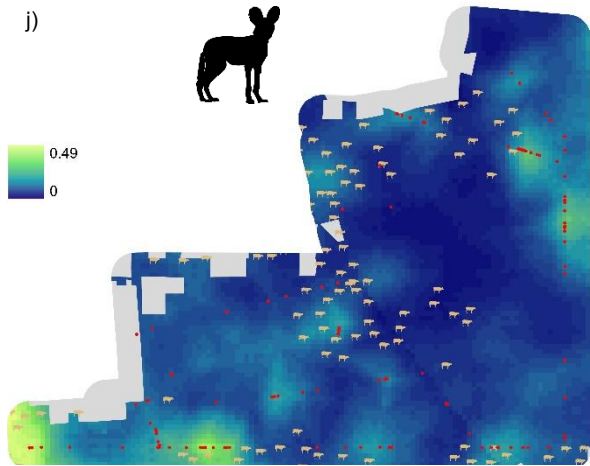
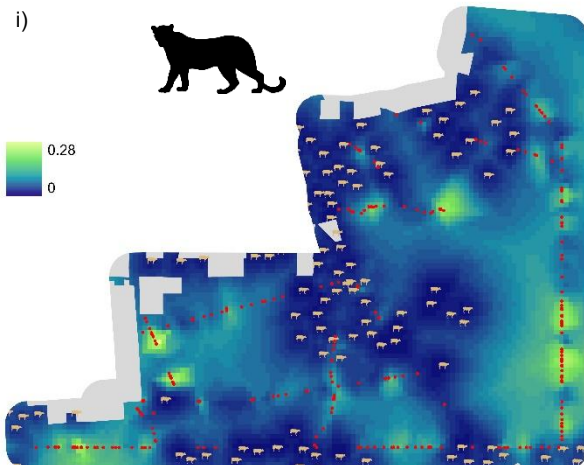
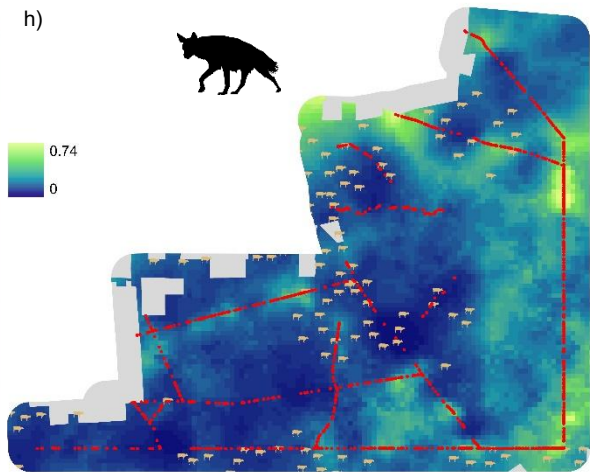
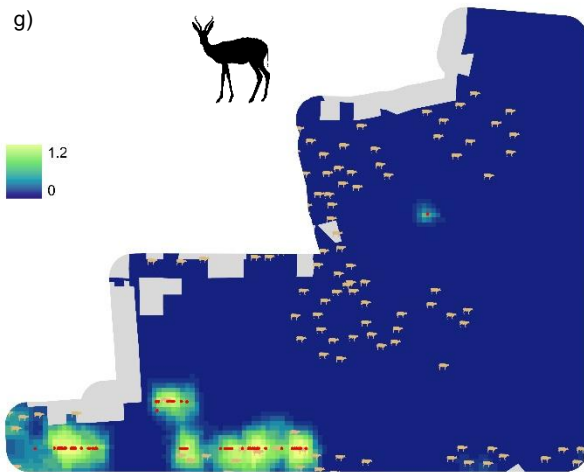
For most species, multiple subset models, and in rare cases the full model, returned similar predictive performance, thus contributing simultaneously to relative track density predictions based on their stacking weights. The binomial components of the hurdle models performed well, with the area under the receiver operating characteristic curve (AUC) values ranging from 0.66 to 0.92 (AUC > 0.7 is considered acceptable). The weighted mean AUC (across retained models) per species was as follows: gemsbok (0.84), greater kudu (0.68), red hartebeest (0.87), ostrich (0.75), blue wildebeest (0.89), eland (0.89), springbok (0.74), African wild dog (0.66), and lion (0.92). The lower performance of the African wild dog model likely reflects their low density and extreme wide-ranging behaviour, introducing greater uncertainty into the data.

For the positive components of hurdle models and Tweedie models, predicted relative track density values showed a central tendency close to the mean observed values for all species, but generally underpredicted the higher observed values. This is unsurprising for ecological data with high dispersion, as models will focus on the smaller values that dominate the dataset. While absolute predicted values are therefore not reliable (nor is that the goal), relative increases in observed values were matched by relative increases in predicted values within the central data range. To further evaluate absolute predictive performance, we assessed whether the mean absolute error (MAE) of predicted values (averaged across retained models) was at least on the same scale as the mean observed relative track density, and ideally smaller. For the positive components of hurdle models, species-specific metrics were (mean observed relative track density, average MAE): gemsbok (3.35, 2.28), greater kudu (2.58, 1.94), red hartebeest (4.60, 3.51), ostrich (1.63, 1.07), blue wildebeest (4.10, 4.13), eland (3.70, 3.12), springbok (3.25, 2.02), African wild dog (1.80, 0.98), and lion (0.75, 0.32). For Tweedie models, we evaluated these metrics separately for zero and positive observed values to avoid misleading interpretations. The mean observed relative track density is typically low due to many zeros, which can make the MAE seem large, even when predictions are reasonably accurate. The species-specific metrics were (for observed zeros: '0', average MAE; for positive observed values: mean observed relative track density, average MAE) : brown hyena (0, 0.16; 0.70, 0.52), leopard (0, 0.03; 0.61, 0.56), cheetah (0, 0.01; 0.82, 0.79), and spotted hyena (0, 0.006; 0.68, 0.67). Similar to African wild dog, we attribute the lower performance of blue wildebeest positive model to its low-density and highly nomadic behaviour (Verlinden, 1994). Note that the positive models for springbok, African wild dog, and lion did not include spatial random effects as datasets display no

spatial autocorrelation. Moreover, the small sample size of springbok positive models ($n=50$) prevented the application of cross-validation with spatial clusters. Instead, MAE was calculated as the mean across 5,000 bootstrap iterations (with replacement at the original sample size) of the model's predictions (see **Appendix 5E** for details on these specific cases).

Figure 5-6 illustrates the predicted relative track density for the 13 target species across the study area, while **Figure 5-7** presents the overall predicted relative density for large carnivores and herbivores (a and c), for which areas of higher wildlife density were identified (b and d). For herbivores and to a lesser extent for carnivores, higher relative density was overwhelmingly influenced by proximity to cattlepost areas. The pan-rich habitat in the southern and western parts of GH11-GH13 appeared to support the largest diversity of both large carnivores and herbivores. The highest densities concentrated in the same area and along the CKGR boundary. In terms of movements, the two ecological corridors between the study area and adjacent WMAs in the south (KD1 and KD5-KD6) appeared functional, particularly the western Corridor 1 (to KD1), which is the largest. However, species-specific preferences exist: brown hyena, gemsbok and possibly eland tend to favour the eastern 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 across the tar road. 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 5-7** b and d). Note that we found no evidence of the well-documented large seasonal movements of blue wildebeest between the WMA pan landscape and the CKGR in response to rainfall (Bonifica, 1992; Verlinden, 1994). However, such movements typically occur during years of below-average rainfall, which only applied to the 2019 surveys. Our survey timing may also have missed these movements, as they are highly dependent on temporally variable local conditions; trackers, in fact, noted wildebeests passing close to Kacgae (GH10) shortly after the end of November 2019 survey.





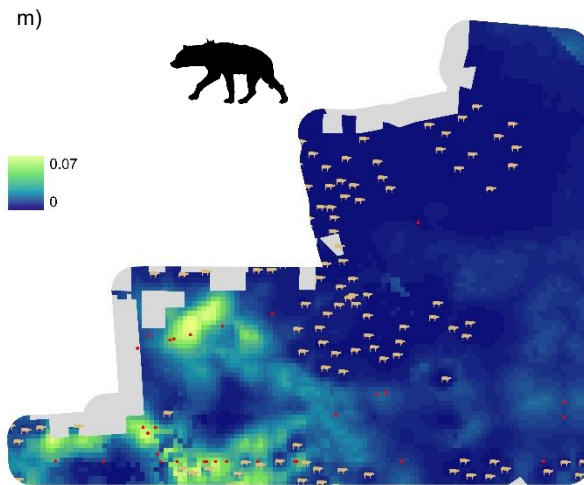


Figure 5-6 Predicted relative track densities per species.

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. Colour gradients are only comparable within each map, not across maps, as predicted relative track density is a spatially explicit, species-specific relative measure - more mobile species are more likely to intersect transects for the same population size, resulting in higher predicted relative track density values. Maps also display the locations of cattleposts, fenced farms, and recorded track sets up to six days old.

Icon sources: African wild dog, brown hyena, cheetah, leopard, spotted hyena from PhyloPic ([CC0 1.0](https://www.phylopic.org/)). Greater kudu from PxHere Team ([CC0 1.0](https://www.pxhere.com/)). 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 & Rob Slotow (vectorised by T. Michael Keesey) from PhyloPic ([CC BY 3.0](https://www.phylopic.org/)). Lion by Gabriela Palomo-Munoz and blue wildebeest by Graham Montgomery from PhyloPic ([CC BY 4.0](https://www.phylopic.org/)).

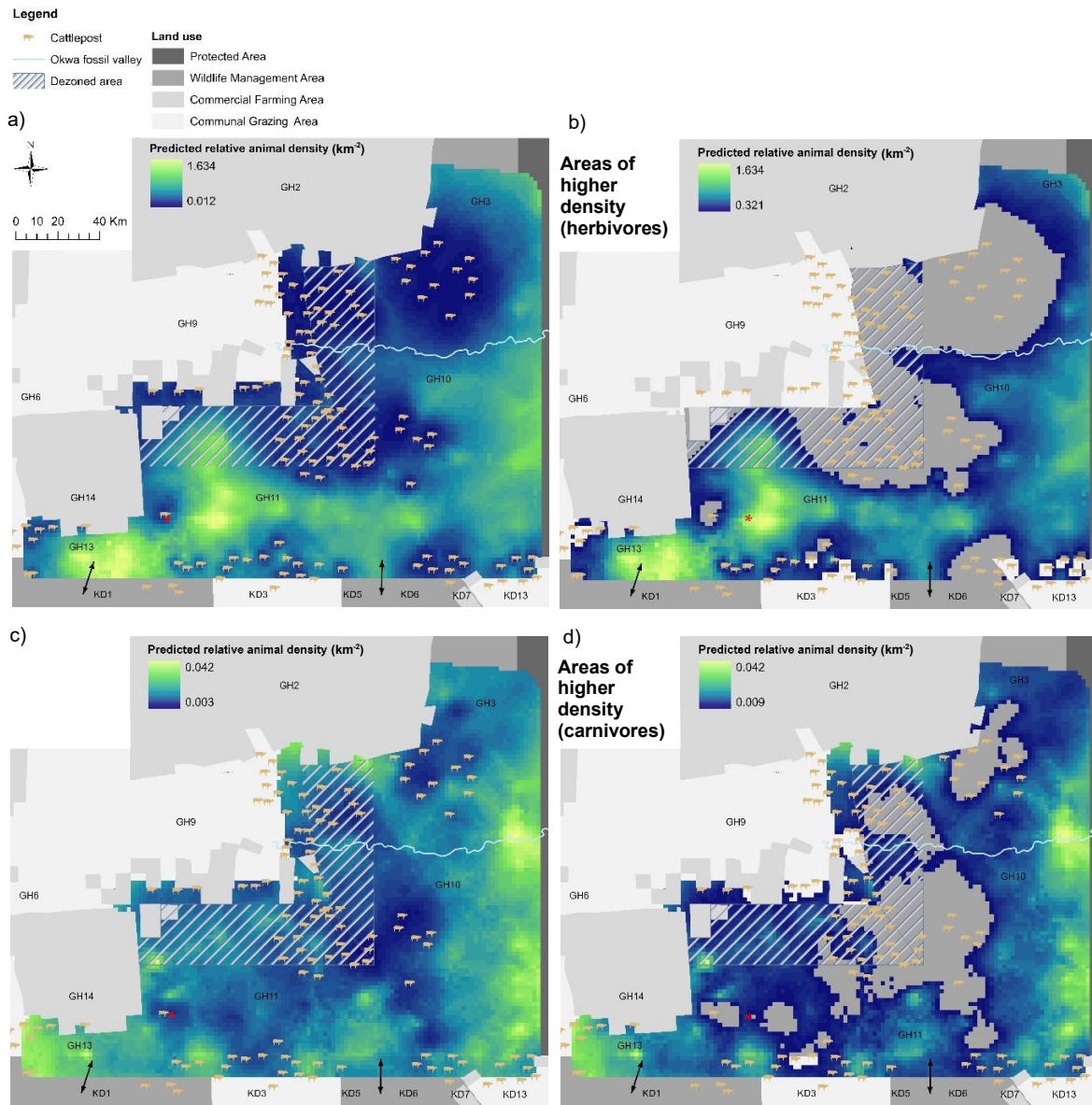


Figure 5-7 Relative animal density for a) large herbivores and c) large carnivores, along with their respective estimated areas of higher relative density in b) and d).

Data were classified with natural Breaks (Jenks) for mapping. Colour gradients are only comparable within each map, not across maps, as predicted animal density is a spatially explicit, guild-specific relative measure. The locations of cattleposts, land use types, dezoned WMA 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 the Corridor 1, while the arrow on the right marks the Corridor 2 - two of the three wildlife corridors identified by CI (2010a) within the Western Kgalagadi Conservation Corridor area.

4. Discussion

Despite its cost-effectiveness (Keeping, Burger, et al., 2018; Seidlitz et al., 2021), the use of indirect animal signs to estimate absolute population densities has often been criticised due to challenges in estimating animal detectability, which can undermine reliability (Dröge et al., 2020; Hayward et al., 2015; Karanth et al., 2003). Index Calibration Survey (ICS) methods have attempted to address this by calibrating track indices to true abundance using independent density measures (Funston et al., 2010; Houser et al., 2009; Stander, 1998; Winterbach et al., 2016). While effective for some species, ICS typically relies on the difficult task of differentiating tracks between individuals (Edwards et al., 2000; Funston et al., 2010), and still faces challenges with detectability and precision (Dröge et al., 2020). In this regard, the approach based on FMP formula addresses detectability issues by inherently accounting for animal detectability along transects and can be corrected for the probability of track detection by observers, if needed (Gielen et al., 2024). Importantly, as a random encounter model, it does not require individual track recognition.

Building on this theoretical foundation, we demonstrate the versatile use of track data, derived from a unique dataset, for generating absolute population density estimates, analysing the impact of environmental variables on relative wildlife density, and determining its spatial variation and potential movement pathways. 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 generates complementary findings.

4.1. Track surveys for population monitoring in wildlife conservation and sustainable use

By surveying nearly all accessible roads in our study area, our sample penetration was approximately 0.5 km per 10 km². This is probably reasonable for species with relatively large daily travel distances, although additional survey effort, particularly in the core of GH10, may improve density estimate precision (though not necessarily its absence of bias) (Keeping & Pelletier, 2014; Stephens et al., 2006), which enhances the ability to assess trends over time (Dröge et al., 2020). Note that confidence intervals will inherently have a certain width due to the uncertainty of $\widehat{M}$, which can vary depending on the data used. In this regard, while findings from Chapter 4 suggest limited seasonal variation in $\widehat{M}$ for some of the large herbivore species we studied, further research is recommended to confirm this. Then, additional off-road

transects, if logistics allow, may improve the independence of transects relative to animal movements, especially for large carnivores that often use roads (Abrahms et al., 2016; Hägerling & Ebersole, 2017). However, Keeping (unpublished data) found no significant difference in density estimates between road and off-road transects in the Kgalagadi WMAs, suggesting animals travel on roads when encountered rather than actively seeking them, except for brown hyenas. As a result, our estimates for this species may be slightly overestimated.

Regarding overall trends, the Kalahari experiences regular drought spells (Tyson, 1980), often causing temporary wildlife declines to which Kalahari wildlife is usually resilient, either through a nomadic lifestyle or physiological adaptations. However, in recent decades, increasing anthropogenic developments have directly affected wildlife populations and also diminished their ability to recover from drought (Child, 1972; Williamson et al., 1988). 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: Bonifica, 1992; DG Ecological Consulting, 2010; DHV, 1980; DWNP, 2015, 2018; Thouless, 1998). In this context, the overall declining tendency of large herbivores in our study area warrants close monitoring. Over the study period, contributing factors likely include the 2018–2019 drought, supported by the discovery of numerous red hartebeest carcasses near transects during the November 2019 survey. Additionally, the massive allocation of new cattleposts between 2015 and 2021 around WMA villages may have further displaced wildlife into the cores of WMAs, as suggested by our predicted species density distribution results (**Figure 5-7 b and d**). However, the wet season 2020–2021 brought above-average rainfall, potentially contributing to the slight recovery observed in some species by November 2021.

In relation to wildlife resources, Botswana reopened trophy hunting in 2019, effective from 2020, intended to provide key income source for remote communities living alongside wildlife (Mbaiwa & Hambira, 2023). At the same time, quotas must be carefully calculated to ensure sustainability. WMAs are the primary zones where hunting quotas are allocated, largely based on aerial surveys conducted by the Government of Botswana since 1987 (DWNP, 2012). However, the last aerial survey took place in 2018, and this method is known to be ineffective for carnivores (Caughley, 1974; Jachmann, 2002). Nonetheless, leopards are included in hunting quotas, while reliable scientific data for most hunting grounds are not yet available. In the four WMAs within our study area, 16 leopards are allocated for 2025 trophy hunting season (Government of Botswana, 2024). This represents 25% (95%

CI: 20–32%) of the local population, which we estimated at 63 individuals (95% CI: 50–81), including the unsurveyed northern portion of GH3. This quota therefore far 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 for leopards is particularly urgent, as they are frequently involved in livestock predation conflicts, which may lead to legal or illegal retaliatory removals, further threatening the population (Swanepoel et al., 2014).

4.2. Track surveys for guiding land use planning

Overall, our models performed relatively well in inferring relationships between relative track density and environmental variables. However, some improvements are possible. The median transect length per grid cell was 2.0 km (interquartile range: 1.47–2.04 km), with a minimum of 0.006 km and a maximum of 4.368 km. Cells with shorter transect lengths are more likely to yield less representative track density estimates. Incorporating cell sampling effort as a covariate for track density variance, a feature under development in the sdmTMB package, might address this issue. Additionally, the models did not account for intraspecific interactions, though these may be more relevant for smaller-scale studies. Predation risk was also omitted from herbivore models, as resource availability in the Kalahari’s sparse, temporally variable landscape likely has a greater influence on large-scale herbivore distribution. Locally, herbivores adapt their behaviour, such as seeking cover (e.g. greater kudu) or using open pans (e.g. blue wildebeest and red hartebeest). Modelling vegetation cover classes in a highly mosaic habitat also remains challenging, particularly in distinguishing shrub and large tree-shrub classes. Despite the good overall accuracy of classification (0.90), refinements could target areas like the GH10 core, which had fewer training points. Lastly, alternative analysis strategies could involve extending the FMP formula into a spatio-temporal Bayesian smoothing model, as demonstrated by Jousimo & Ovaskainen (2016) to estimate variation in population density over space and time. However, this approach would rely on limited fresh tracks, likely causing convergence issues, as noted by the authors when working with sparse data. Despite potential improvements, intrinsic individual animal choices among equivalent movement options will always introduce variation. This is especially true for highly generalist species (e.g. leopards), wide-ranging species (e.g. African wild dogs), or nomadic species (e.g. blue wildebeest), making their modelling inherently more challenging. Low-density species (e.g. lion) pose additional challenges, best addressed through increased sampling effort and survey repetition. As observed by Verlinden

and Masogo (1997), variable relationships with rare species may lose significance due to many unoccupied yet suitable habitats.

Despite these limitations, our findings on the impact of environmental variables on species-specific relative track density (as a proxy of species relative density) generally align with existing literature. Half a century ago, DHV (1980) identified three key factors influencing large herbivore distribution in the Kalahari: (1) distribution of mineral nutrients in plants and soil, (2) distribution of man and livestock, and (3) rainfall. In line with this, we also highlight the importance of burned areas for most herbivores, as they provide nutrient-rich grass during regrowth. Among these factors, the presence of cattleposts appears particularly important, with all species negatively affected, except springbok, African wild dog, and to a lesser extent cheetah. Uncontrolled grazing by overstocked cattle herds currently practiced in the area reduces grass cover while increasing unpalatable grasses and shrub density (Skarpe, 1986; Verlinden, 1997). Goats may further degrade browse quality (Bergström & Skarpe, 1999), and cattle-associated flies may deter large herbivores (Indigenous trackers, pers. comm.). These create unsuitable habitats for most large wild herbivores, particularly grazers. However, vegetation degradation is typically observed within 10 km of cattleposts (Skarpe, 1986; Verlinden et al., 1998), while we observed that gemsbok starts appearing beyond 20 km and eland presence increases steadily with distance. This pattern may result 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, while red hartebeest and blue wildebeest exhibit intermediate tolerance, apparently using livestock areas rather as transit zones (Ngwamotsoko, 1985). On the other hand, large carnivores are likely primarily driven away by farmer hostility following 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, 2021b). Despite this, African wild dogs appear to continue to transit through cattlepost areas, possibly explaining their ranking as the top conflict species.

Our results on relative wildlife density distribution also closely align with the comprehensive occurrence probability modelling by Keeping et al. (2022a) across the WKCC, despite using independent track datasets and different analytical methods. This congruence enhances confidence in our findings. The most notable difference is the relatively high occurrence probability predicted by Keeping (2022a) for lions, spotted hyenas, and elands in the western part

of Okwa valley (GH10), where we found little to no tracks. This discrepancy may reflect a temporal range shift, as Keeping's study used 2008–2018 data, while most cattleposts near the Okwa valley were developed between 2015 and 2021. In fact, approximately 75% of all cattleposts within the four WMAs at the time of our study were established during this period, primarily in GH3–GH10. Consequently, species like spotted hyena, springbok, and blue wildebeest, which Keeping et al. (2022a) predicted to occur more widely in GH3–GH10, were only rarely recorded there in our surveys. While it is possible that the above-cited species were more present during unsurveyed months, off-road track surveys conducted in the GH3–GH10 core in May–September 2022 and March–April 2023 confirm our predicted distribution for all species (CCB, 2025). Another appreciable difference is that Keeping et al. (2022a) predicted a medium-low probability of lion presence in GH11–GH13, whereas we recorded virtually no tracks over three years of surveys. Farmers in the area also reported that transient lions were detected only on rare occasions (pers. comm.).

Additionally, Keeping et al. (2022b) conducted a state-of-the-art landscape connectivity analysis across the WKCC, predicting the complete loss of connectivity between the CKGR and KTP for three disturbance-sensitive species —gemsbok, eland, and lion— if all proposed agricultural developments are implemented. This includes full cattlepost development 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 5-7**). Since Keeping et al. (2022b)’s study, much of the cattlepost development has been completed, leading to the apparent loss of connectivity for lions and potentially for eland as well (**Figure 5-6 f and l**). In line with this, the collaring of five lions in GH10 between 2023 and 2025 did not reveal any movements into GH11 (Kaileigh Henry, pers. comm.). The authors proposed an alternative land-use strategy, recommending moving a limited number of cattleposts encroaching on critical wildlife corridors to alternative development zones within the same WMAs. Many of these recommendations were adopted in the Integrated Land Use Management Plan (ILUMP) for Ghanzi and Kgalagadi Districts (Tshukudu, 2024). In our study area, this primarily involves relocating the southernmost cattleposts of Bere and Kacgae villages to improve connectivity across the tar road between GH10 and GH11, which still appears the key gateway linking the eastern and western WMAs (**Figure 5-7**). Additionally, ensuring the absence of cattleposts or settlements outside designated zones, such as Ranyane, would further enhance connectivity in the western Corridor 1 (**Figure 5-7 b and d**). A 5 km conservation buffer along the Okwa valley has also been proposed to protect its cultural heritage (DNMM, 2022), and would benefit several species such as

the vulnerable IUCN red-listed cheetah (**Figure 5-6 k**). However, the planned dezoning of northern GH11 would result in the loss of significant habitat for many large carnivores and herbivores (**Figure 5-7 b and d**). Lastly, we emphasise the critical importance of the small GH13 WMA, which supports several large pans, one of the highest abundances of large wildlife of the study area and main potential route towards the KTP. As of now, cattlepost allocation around WMA villages remains ongoing, with at least 11 additional cattleposts developed since 2021 (pers. obs.).

4.3. Track surveys with and for communities globally

A similar study could have been conducted using alternative methods such as camera trapping or, to a lesser extent, aerial surveys. However, this 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 potentially engaging local community members with advanced tracking skills. Besides providing much-needed employment, track-based work also helps preserve and transmits these rapidly eroding skills, thereby valuing cultural identity and Indigenous knowledge (Aswani et al., 2018; Legge et al., 2024; Liebenberg, 2021). In the Kalahari, the traditional ecological knowledge of San community members is now being integrated into research projects in collaboration with local Non-Governmental Organisations (NGOs) (Finerty et al., 2024; Gielen et al., 2024; Kalahari Camelback Trackers Project: <https://tanate.org/kalahari-camelback-trackers/>). As with camera traps (e.g. Dickman et al. (2025)), tracking could also be incorporated as a monitoring tool into Conservation Performance Payment (CPP) programs or used in other Payments to Encourage Coexistence (PEC) initiatives, thereby including trackers as an additional community group in conservation efforts. These initiatives allow communities to benefit directly from wildlife conservation, potentially fostering coexistence and renewed appreciation for wildlife (Dickman et al., 2025; Dickman et al., 2011; Hamm et al., 2025). In the Kalahari, where climate change increasingly undermines the viability of cattle farming, they offer a promising avenue for livelihood diversification (Perkins, 2019). Such partnerships can potentially contribute to long-term ecological, cultural, and local economic benefits, while helping supporting 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, sand) and tracking knowledge are widely available. Tracking skills, for example, are present in Siberia (Brandišauskas, 2016), Canada (Wong et al., 2011), Brazil

(Dario, 2019), India (Lohe, 2014), or Philippines (Hagen et al., 2016), to cite a few. Recently, the FMP approach itself has also been applied elsewhere such as 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 of Canada (Doran-Myers et al., 2021), Bulgaria (Popova et al., 2019) or China (Gu et al., 2018), or eastern African savannahs (Osipova et al., 2019). 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 km²) over the past two decades (Legge et al., 2024). While data collection currently focuses on presence-absence of animal signs, testing the FMP approach to estimate population abundance would warrant further investigation. Indigenous Peoples manage or hold tenure rights over a quarter of the world's land surface, intersecting with 40% of terrestrial protected areas and ecologically intact landscapes (Garnett et al., 2018). While 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. This highlights significant potential for developing conservation programs integrating Indigenous knowledge.

5. Conclusion

The FMP approach has been tested through several simulation studies and against other common field monitoring techniques, generating essentially unbiased population density estimates (Jousimo & Ovaskainen, 2016; Keeping, Burger, et al., 2018; Keeping & Pelletier, 2014; Stephens et al., 2006). However, this unbiasedness is primarily contingent on the accuracy of $\bar{M}$ across both space and time, which remains the primary limitation of the FMP (Prosekov et al., 2023; Stephens et al., 2006), and warrants further investigation. Additionally, the confidence intervals of the population density estimates remain less robust, especially for rare, social, or territorial species, potentially complicating population trend assessments (Jousimo & Ovaskainen, 2016). Bayesian spatio-temporal extension of the FMP formula (Jousimo & Ovaskainen, 2016) as well as improved transect design and effort (Finerty et al., in prep) could help address this issue. Despite these potential challenges, our work successfully demonstrated the broader applicability of track surveys using the FMP approach and their value in land-use planning - a method that can be replicated wherever suitable tracking substrates and skills are available.

With regards 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 protected areas. Its multi-use areas hold as much, if not higher, value for wildlife than those within protected boundaries (DWNP, 2015, 2018; Keeping, Keitsile, et al., 2018). Therefore, the region holds significant potential for a nature-based economy, which can coexist with cattle farming only through a low-density, rotational grazing approach. Sedentary intensive farming is ill-suited for the area and often leads to environmental degradation due to poor management practices. The Kalahari also boasts an incredible cultural heritage, with Indigenous knowledge developed over thousands of years, although rapidly disappearing. Despite the many reports and policies spanning over more than half a century (Campbell, 1997; Cooke, 1985), efforts to preserve and sustainably develop the region have faltered due to complex interactions and diverging interests between political, economic, and social spheres. However, the recent ILUMP initiative takes a holistic approach, integrating high-quality scientific data and input from various socio-economic groups and communities to propose a balanced compromise. Our study supports these efforts, and we encourage government bodies and stakeholders in land use planning to lead by example in enforcing smart land-use planning that benefits in the long-term both ecosystems and well-being of the communities dependent on them.

Supplementary material

The Cybertracker application for track surveys (**Appendix 5A**), the note on the spatial layers creation in ArcGIS 10.8. (**Appendix 5B**), the Google Earth Engine script for creating the vegetation cover map (**Appendix 5C**), the one for creating the vegetation index maps (**Appendix 5D**), and R scripts for modelling species relative track density and predicting its distribution (**Appendix 5E**) are available in the Supplementary Material.

