

Chapter 4

Refining population density estimation from track counts: Improving daily travel distance estimates through trailing of large herbivores in the Kalahari, Botswana.

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Abbreviations

AICc	Akaike Information Criterion corrected for small sample sizes
BCa	Bias corrected and accelerated
CKGR	Central Kalahari Game Reserve
CTSD	Continuous-time speed and distance
$\hat{D}$	Population density estimate
FMP	Formozov-Malyshev-Pereleshin
GPS	Global Positioning System
KGR	Khutse Game Reserve
$\hat{M}$	Daily travel distance estimate
$\hat{p}_1$	Probability that the animal movement paths intersect with the transect at least once
$\hat{p}_2$	Probability of track detection by the observers
S	Total transect length
x	Observed track count
$\hat{x}$	Estimated track count
$\frac{\hat{x}}{S}$	Estimated track index

Glossary

Track: animal footprint on the substrate. More particularly in this manuscript, “track” represents the result of an intersection between an individual animal movement path and a transect; although appearing as series of footprints on the latter, this intersection is conceptualised as one individual track interception.

Trail: series of footprints of a same individual animal, representing its movement path across the landscape.

Track survey: method detecting and collecting the geolocation and characteristics of animal track interceptions found along transects of defined length within a study area.

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Author contributions

MCG and AA conceived the ideas, designed methodology with the help of DK, and supervised data collection; MJ, SP, SM, XS, DS, MCG, PI, TG, AA collected the data; MJ, SP, MCG processed the data; MCG, MJ, NS, AA analysed the data; MCG created the artwork and led the writing of the manuscript and AA, DK and NS revised it. All authors contributed critically to the study and gave final approval for publication. Our study brings together authors from a number of different countries, including scientists and expert trackers based in the country where the study was carried out. We engaged with local holders of Indigenous knowledge to design the data collection protocol to ensure that diverse sets of perspectives were considered and our study design could successfully collect the required data.

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Data availability

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

Declarations**Ethics approval and consent to participate**

The research only involved non-invasive trailing and track surveys of herbivore individuals or groups; therefore, ethics and animal welfare approvals were not required. However, we took great care to minimise animal disturbance. Any observer-induced behaviour in the animals (e.g. running away upon approach) resulted in the trailing to be suspended until the observer's presence would not affect the animals anymore. All research activities were implemented in agreement with the instructions from Botswana's Department of Wildlife and National Parks under the Research Permits ENT 8/36/4 LV (13) and ENT 8/36/4 XLVI (32).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Abstract

Background: Animal track surveys can enable rapid population monitoring for conservation, contingent on a suitable substrate and highly skilled trackers. The Formozov–Malyshev–Pereleshin (FMP) formula converts track counts along transects into absolute population density estimates, using the species' average daily travel distance estimate ($\bar{M}$). The accuracy of $\bar{M}$ is currently one of its main limitations. If empirical $\bar{M}$ from the study region is not available, $\bar{M}$ can be estimated allometrically, but less precisely, through body mass- $\bar{M}$ scaling rules. The present study explores ways to better estimate both empirical and allometric $\bar{M}$ in order to improve the accuracy of density estimates.

Methods: We tested a cost-effective methodology to collect high-quality empirical $\bar{M}$ through trailing of five herbivore species with local certified trackers, using the Kalahari, Botswana, as a study site. Since allometric $\bar{M}$ are underestimated in the Kalahari, we explored their calibration using existing empirical $\bar{M}$ and new data from this study. Finally, we integrated our findings to generate population density estimates from track surveys using the FMP formula approach.

Results: Through trailing, we provide empirical $\bar{M}$ for these five herbivore species, which previously lacked data for the area. While confirming the temporal stability of daily travel distance values within the study season, we encourage further research to assess the need of time-specific $\bar{M}$. We derived two separate coefficients to directly correct allometric $\bar{M}$ for Kalahari species, based on their foraging strategies. Based on our interpretation of the density estimate results, we discuss the importance of the spatio-temporal accuracy of $\bar{M}$, transect design, and survey effort in population monitoring.

Conclusion: Our research delivers new elements to strengthen the use of track data for wildlife monitoring in low-density environments. We also highlight opportunities to integrate Indigenous knowledge with modern technology in research, fostering collaboration with local communities for mutual benefit.

Keywords daily movements; track survey; Indigenous knowledge; wildlife abundance; Formozov–Malyshev–Pereleshin formula.

I. Background

Conservation of natural ecosystems is currently a global priority, as the Earth is facing an unprecedented environmental crisis (Barnosky et al., 2011; Jhariya et al., 2021). It requires robust tools to assess the ecosystems' current status and evaluate progress made towards their long-term functionality. Wildlife populations are relatively direct indicators of ecosystems' health and, therefore, techniques monitoring their abundance provide essential data towards a better understanding of conservation strategic priorities (Johnston et al., 2015; Nichols, 2014). As counting all individuals of a population is rarely achievable, practitioners rely on estimations (Iijima, 2020; Schwarz & George, 1999). Methods based on direct observations may be difficult to apply to some species targeted by conservation programs due to their usual low density or elusive behaviour. On the other hand, methods based on indirect observations (e.g. footprints, droppings, bait take, camera-trap images) are often more powerful in detecting animals, less invasive and easier to implement in a diverse range of habitats (Keeping, Burger, et al., 2018; Sadler et al., 2004; Wilson & Delahay, 2001).

Animal track survey is one of the techniques relying on indirect observations, which we define here as the detection, geo-location, species identification and count of animal tracks across sampling units (Funston et al., 2010; Keeping, 2014; Pellikka et al., 2005). The main prerequisite is a soft and clear enough substrate for animals to leave track impressions on the ground. In such a case, the advantage of track surveys over other techniques lies in their ability to cover large areas while simultaneously surveying multiple species, even if rare, cryptic, or nocturnal, without impacting animals (Ahlsvede et al., 2019; Helle et al., 2016; Keeping, 2014). They also return higher encounter rates per sampling effort at a lower cost (Keeping, Burger, et al., 2018; Romani et al., 2018; Seidlitz et al., 2021; Silveira et al., 2003). However, track surveys require highly skilled observers for track identification. Contrary to being an obstacle, this can be a great opportunity for local community members with highly-developed tracking skills to be involved in and benefit from research and conservation projects (Elbroch et al., 2011; Liebenberg et al., 2017; Lilleyman et al., 2022; Southgate & Moseby, 2008).

Due to the difficulty in measuring individual animal detectability, track counts have most often been used as indices of relative abundance (Engeman et al., 2001; Hayward et al., 2002; Kendall et al., 1992; Silveira et al., 2003). For conversion into absolute estimates of population size, they commonly require individual animal recognition (Becker et al., 1998; O'Neil & Swanson, 2010;

Sharma et al., 2005; Sulkava, 2007), calibration to true abundance (Funston et al., 2010; Houser et al., 2009), or specialised modelling (Thorn et al., 2011). Although such methods may work well for specific areas, time periods, or species, they often lack broad applicability or still face issues regarding detectability or density estimate precision (Dröge et al., 2020; Hayward et al., 2015; Karanth et al., 2003). However, a lesser-known approach has a great potential for extended application of track surveys: the Formozov-Malyshev-Pereleshin (FMP) formula. Originally applied to the snowy regions of Russia for a century (Chelintsev, 1995; Formozov, 1932; Stephens et al., 2006), it has been recently introduced to the sandy Kalahari (Ahlsweide et al., 2019; Keeping, 2014), mud and clay soils in Europe (Romani et al., 2018), and tropical forests (Esbach, 2023). The FMP operates as a random encounter model based on the probabilistic intersection (track encounter) of lines of known lengths (transects and animal movement paths). Its mathematical derivation is presented as follows:

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

where, for a given species, estimated counts of fresh (≤ 24 hours old) tracks ($\hat{x}$) along linear transects of total length S (i.e. track index $\frac{\hat{x}}{S}$) are converted into population density estimates ($\hat{D}$) using the average estimated distance the animals travel in 24 hours ($\hat{M}$). To obtain population abundance, $\hat{D}$ is simply multiplied by the total size of the study area (in km^2). So, provided animal movements are independent of transect placement, the presence of more individuals will, on average, result in a higher track index. However, to be converted into absolute population density, the track index should be modulated by $\hat{M}$, as a species travelling longer distances daily should intersect transects more often than a sedentary species. Therefore, $\hat{D}$ is proportional to $\frac{\hat{x}}{S}$ and also inversely proportional to $\hat{M}$. Regarding track detectability, two components must be accounted for $\hat{D}$ to qualify as an absolute estimate: the probability $\hat{p}_1$ that animal movement paths intersect with the transect at least once, so that tracks are left to be recorded, and the probability of track detection $\hat{p}_2$ by the observers (Gielen et al., 2024). $\hat{p}_2$ (either measured or assumed close enough to 1) directly corrects the observed track count (x) to return the estimated track count $\hat{x}$. Meanwhile, $\hat{p}_1$ is inherently measured through all the FMP parameters, provided all tracks are recorded regardless of individuals' identity (see **Appendix 4A** for a detailed demonstration on how track detectability is embedded in the FMP equation). Ignoring animal individual identity is necessary to ensure that $\hat{D}$ remains

unaffected by the tortuosity of animal movement paths (Keeping & Pelletier, 2014).

As $\frac{\pi}{2}$ and S are exact values, and $\hat{x}$ is an estimate corrected by $\hat{p}_2$, the most important parameter left to impact the accuracy of $\hat{D}$ is the accuracy of $\hat{M}$. Obtaining quality $\hat{M}$ relevant to the survey's location and time period of the year is currently the main practical limitation to the FMP approach. Empirical $\hat{M}$ are commonly derived from movement data collected within the study area, or the ecological region it belongs to, using Global Position System (GPS) devices fitted on the animals (McQualter et al., 2015; Stander, 1998; Webb et al., 2010). Although collecting large amounts of data, such a method is expensive and invasive (requiring capture and handling). Consequently, it is often applied to a limited number of individuals, potentially limiting the sample size (each collared animal bringing only one truly independent observation) (Hebblewhite & Haydon, 2010). Furthermore, it may underestimate $\hat{M}$ if GPS fix frequency is too low (Johnson & Ganskopp, 2008; Rowcliffe et al., 2012). Alternatively, $\hat{M}$ can be obtained by visually following habituated animals (Begg et al., 2005; Mills, 1990), or via thread trailing (Hailey & Coulson, 1996). These techniques provide much finer-scale estimates but are limited to a few specific populations. In areas with suitable substrate, high-resolution $\hat{M}$ can be obtained by trailing animals (i.e. following the footprints of an individual or group to reconstruct its movement path across the landscape) forward (Keeping & Pelletier, 2014; Viljoen & Bothma, 1990) or backward using recent rain (Keeping & Pelletier, 2014) or snow falls (as performed by Becker et al. (1998)); a technique requiring highly skilled trackers.

The sandy soil of the Kalahari ecosystem in southern Africa, coupled with the Indigenous tracking knowledge still present among some local community members, makes the region particularly well-suited for track-based wildlife monitoring techniques as well as trailing techniques. Therefore, the FMP has now been applied in the Kalahari for more than a decade, successfully validated against independent measurements of density (Keeping, Burger, et al., 2018). However, despite its increased use, empirical $\hat{M}$ are currently available for a limited number of species only (Ahlsweide et al., 2019; Keeping, 2014). For other species, $\hat{M}$ is calculated allometrically through a scaling rule with the species' body mass (Carbone et al., 2005). However, this approach tends to underestimate $\hat{M}$ for Kalahari species, resulting in an overestimation of $\hat{D}$; a bias currently requiring $\hat{D}$ to be corrected by a unique factor developed by Keeping (2014). However, we argue that certain species groups may travel greater distances daily

depending on the specificities of their ecologies (i.e. requiring different correction factors), particularly in relation to the sparse and patchy distribution of resources in the Kalahari.

Our study harnesses the region's assets to directly address these challenges. Specifically, we aim to answer the following question: How can we improve both empirical and allometric estimates of species' average daily travel distance to enhance the accuracy of $\hat{D}$? By collaborating with local certified trackers, we developed a cost-effective non-invasive forward trailing method to rapidly obtain high-quality daily travel distance estimates. The method was applied during the cold dry season on five Kalahari herbivore species that previously lacked empirical $\bar{M}$ values. Additionally, for each species, we assessed the temporal stability of daily travel distance values throughout the season, a prerequisite for computing their average estimate for this time period. We integrated our data with existing empirical $\bar{M}$ of Kalahari mammal species to derive new coefficients for directly adjusting allometrically-derived $\bar{M}$, considering differences in species ecology. Lastly, we applied our findings to the FMP formula to generate density estimates from track counts of 11 herbivore species, and identified gaps for future research.

2. Methods

2.1. Study area

The study area is located in two protected areas of Botswana: Khutse Game Reserve (KGR) and the southern part of Central Kalahari Game Reserve (CKGR). The trailing and track survey study areas cover approximately 3900 km² and 2800km² respectively, located between 23°–24°S and 024°–025°E (**Figure 4-1**). They are part of the semi-arid Kalahari Desert (hereafter referred as the Kalahari), an ecological region covering large parts of Botswana, Namibia and South Africa. It is almost entirely mantled by sand, where grasses, shrubs and scattered trees form a more or less open savannah depending on local climatic and soil variations (Skarpe, 1986; Weare & Yalala, 1971). Annual rainfall averages 400 mm (LEC, 2024), occurring almost exclusively during the rainy season between November to April (DHV, 1980). Isolated clay depressions known as pans are the only source of surface water after rains, and such free water is highly ephemeral (Lancaster, 1974). However, four permanent artificial waterholes are supplied all year round for wildlife use. Due to the Kalahari's harsh conditions and limited resource availability, wildlife is present in lower density compared with the country's northern wetlands (DWNP, 2015, 2018). Animals are relatively free-ranging

except for the presence of a double game fence along the southern and eastern borders of KGR, however permeable due to numerous holes along its length (Kesch et al., 2014). The road network is sparse, with 550km of sand roads used by tourists and park management officials.

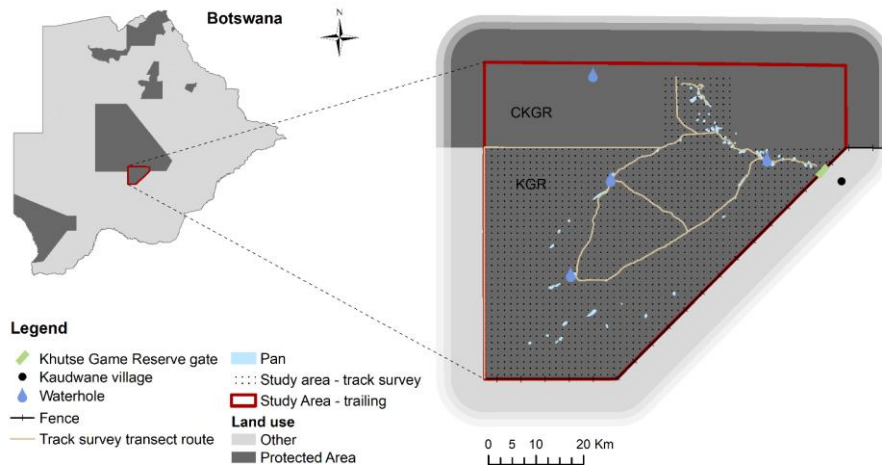


Figure 4-1 Trailing and track survey study areas.

The trailing study area comprises Khutse Game Reserve (KGR) and a southern portion of the Central Kalahari Game Reserve (CKGR), both protected areas situated in the Kalahari Desert, Botswana. Track surveys were conducted within KGR and a small portion of CKGR, where they sample 59% of the existing sand roads.

2.2. Forward trailing protocol and calculation of empirical $\hat{M}$

We collected daily travel distances for five Kalahari large and medium-size herbivore species: eland (*Taurotragus oryx*), red hartebeest (*Alcephalus buselaphus caama*), greater kudu (*Tragelaphus strepsiceros*), springbok (*Antidorcas marsupialis*), and ostrich (*Struthio camelus*). To ensure data of high spatial resolution, we developed a two-day forward trailing approach inspired by Keeping & Pelletier (2014), in consultation with local expert trackers based on their knowledge of animal behaviour (**Figure 4-2**). On day 1, individuals or groups of the species of interest (thereafter referred as the target) were opportunistically spotted from a vehicle, predominantly along existing roads around midday or in the afternoon. While keeping animal disturbance to a minimum, the following data were recorded using a custom-made CyberTracker (<https://cybertracker.org/>) application on a smartphone: date and spotting time, GPS location of the target, species, number of individuals, their sex and age class, their behaviour and a photograph. Such information was collected to facilitate the identification of the trailing starting

point the next day. When multiple targets were spotted, we selected which one to trail based on the quantity and spatio-temporal distribution of the data already collected. We aimed to achieve an even distribution within and between species while avoiding re-sampling the same targets. On day 2, the selected target was trailed from the location it was originally spotted on day 1, starting a minimum of 4 hours before the spotting time on day 1. The trailing path was recorded with the same CyberTracker application while walking exactly along the animal footsteps, using a GPS fix frequency of 1 second. The trail was ended where the target was re-sighted, or just fled upon the field team's approach, at the same time it was spotted the previous day, ensuring the recording of a 24-hour trail. If the target was not met on time, trailing was pursued when possible, until trackers estimated that 24 hours of travel distance had been sampled based on the trail's freshness. The data collection protocol is explained in detail in **Appendix 4B**. A description of our CyberTracker application is also available in **Appendix 4C**.

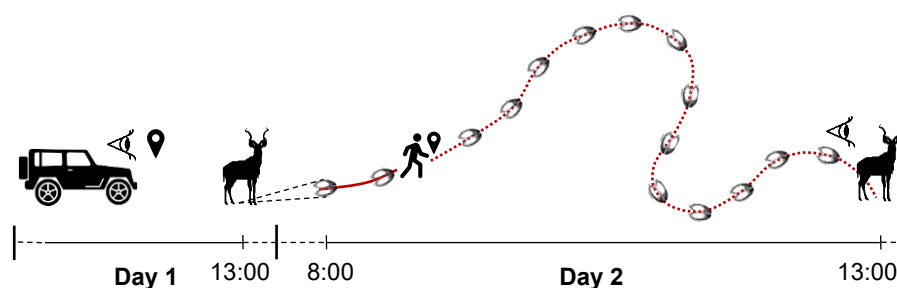


Figure 4-2 Illustration of the forward trailing method we developed to collect species 24-hour travel distances.

On the first day, the animal(s) is spotted at a given time and location. On the second day, the same animal(s) is trailed forward (red line) from the location it was spotted on day 1, until observers catch up with it at the same time it was spotted the day before. There, the animal(s) is ideally re-sighted or the place from where it just fled upon the observers' approach is located.

Icon sources: Greater kudu by PxHere Team ([CC0 1.0](https://creativecommons.org/licenses/by/4.0/)), Jeep by Isaac haq from Noun project ([CC BY 3.0](https://creativecommons.org/licenses/by/4.0/)), Eye by dh park from Noun project ([CC BY 3.0](https://creativecommons.org/licenses/by/4.0/)), person and pin from Microsoft Corporation 2019, greater kudu track from Liebenberg (1990a).

Data collection took place between the 15th May and the 15th August 2023. Observers consisted of two data recorders and three Indigenous trackers from the Kaudwane community. Two trackers were certified as Trailing Professional, and one was certified as Trailing Level III (CyberTracker Conservation's Tracker Certification System (2018)). Trackers led the trailing, followed by a recorder with the CyberTracker GPS logging application. For safety and logistical reasons, a vehicle followed the team on foot from a

distance to minimise noise disturbance. A second recorder stood on the vehicle's roof to enhance the chance of detecting the target towards the end of the trailing.

Following fieldwork, trails were exported and cleaned of irrelevant GPS fixes (i.e. corresponding to a pause in the trailing) in ArcGIS 10.8. Additionally, they were examined for biases related to (1) sampling the target's movements for less than 24 hours, (2) observer-induced behaviour in the target, and (3) estimating the completion of the 24-hour sampling period when the target was not re-sighted on time. Trails with biases were either corrected where possible or, in rare cases, discarded (refer to **Appendix 4D** for details on data curation). Following these adjustments, we computed an empirical $\widehat{M}$ for each species by calculating the average length and standard deviation on the species' final dataset of trails.

2.3. Temporal stability in daily travel distance

We checked for a temporal trend in the daily travel distance values for each species over the three-month data collection period. The absence of such a temporal trend is a prerequisite to the computation of an average $\widehat{M}$ at the species level that is meaningful for the region and the season. For each species, we fitted a linear regression to the daily travel distance data as a function of the number of days since the start of the data collection period, i.e. 16th May being day zero and 15th August being day 91. Model diagnostics were conducted by visually inspecting models' residuals.

2.4. Correction coefficient for allometric $\widehat{M}$ of Kalahari species

We extended the dataset of empirical $\widehat{M}$ collected for the five large herbivores species in this study with existing data for other Kalahari species, totalling 9 Artiodactyla and 11 Carnivora species (**Table 4-1**). Only species with high-quality empirical $\widehat{M}$ available were included, i.e. those obtained from either trailing, visual follows of habituated animals, or GPS tagging with a minimum of 1-hour fix interval. For each of the 20 species, an allometric $\widehat{M}$ (in km) was predicted through a scaling rule with the species body mass (in kg), emulated using data from a variety of species across different biomes:

$$\ln(\widehat{M}) = \beta_0 + \beta_1 \cdot \ln(\text{mass}) \quad (2)$$

with $\beta_0 = -0.11$ and 0.147 and $\beta_1 = 0.26$ and 0.421 for Artiodactyla species ($n=22$) and Carnivora species ($n=39$) respectively (Carbone et al., 2005). In the absence of a scaling rule for birds, we classified ostrich as part of the Artiodactyla

order due to its cursorial locomotion and predominantly plant-based diet. In the same vein, we classified aardvark (*Orycteropus afer*) as part of the Carnivora order.

With this extended dataset, we computed a correction coefficient to adjust the allometrically-derived $\widehat{M}$ of Kalahari species, in order to account for deviations due to specificities in their ecology. To do so, we fitted linear regressions to the 20 species-specific empirical $\widehat{M}$ data as a function of their allometric counterparts, while considering co-variables that might interact with this relationship. In particular, for a same body mass within a given order (i.e. Artiodactyla or Carnivora), some species may travel more than other due to factors mainly linked to their feeding ecology, sociality, or evolutionary path (Carbone et al., 2005; Garland, 1983; Hubel et al., 2016; Morales et al., 2010). Therefore, we split the 20 species into two groups according to their primary “foraging strategy”: social hunters and scavengers (group A), known to travel extensively in their search of food (Hubel et al., 2016; Mills, 1990), versus other strategies such as herbivores and solitary hunters (group B) (**Table 4-1**). Three linear regression models were compared using model selection based on the Akaike Information Criterion corrected for small sample sizes (AICc) (AICcmodavg package in R statistical software version 4.3.2): one with a slope differing between the two foraging strategy groups, one with a common slope for all 20 species, and a null model with no effect of allometric $\widehat{M}$ on empirical $\widehat{M}$. We forced the intercept of the regressions to zero, representing the theoretical limit case of a non-moving species where both allometric and empirical $\widehat{M}$ values are zero. Model diagnostics were conducted by visually inspecting models’ residuals.

2.5. Case study: track survey and FMP density estimation

Track surveys were conducted over 12 months, covering both the wet season 2021-2022 and dry season 2022. Every month, the same set of transects (existing roads) were driven once, totalling 255 km per month. Data collection was implemented from a moving vehicle, with Indigenous trackers acting as observers to record animal tracks. The detailed protocol, described in Gielen et al. (2024), was executed by a single survey team and refined to maximise the probability of detecting existing tracks ($\hat{p}_2$), which assumed to approach 1: the survey, performed exclusively in the morning, focused solely on fresh tracks and involved three trackers (on seats placed in front of the bonnet and on the vehicle’s roof) instead of two. The three trackers, originated from the Kaudwane community, were certified by a mean $\pm$ SD Track & Sign score of 98.0 ± 1.75 % by CyberTracker Conservation’s Tracker Certification System (Liebenberg et al., 2018). All transects were covered with clear sand devoid of

vegetation, making the fresh tracks of the target species easily detectable. Therefore, it is highly unlikely these tracks were missed by full-time trackers with several years of experience in research projects.

Furthermore, surveying during early morning hours avoids disturbance from other vehicles and glare from the midday sun. Finally, transects were surveyed only if they had not experienced rainfall, strong winds, or vehicle traffic in the 24 hours preceding the survey. Upon detection, animal tracks from the previous 24h were logged on a CyberTracker application on a smartphone, recording date and time, species, number of individuals, their sex and age class, and GPS location.

For 11 small to large herbivore species, track counts recorded along transects were converted in density estimates per season (wet and dry) through the FMP formula. When empirical $\widehat{M}$ were not available, corrected allometric $\widehat{M}$ were used. The estimate of density was calculated through the direct input of the parameters' values within the formula. The uncertainty around the estimate was calculated as bias corrected and accelerated (BCa) 95% confidence intervals via non-parametric bootstrapping (Efron & Tibshirani, 1993) (see steps in Keeping (2014)), using R (version 4.3.2). In this process, each transect within each season was treated as independent even if repeatedly sampled each month.

Table 4-1 Dataset of species-specific empirical $\widehat{M}$ and allometric $\widehat{M}$ used to generate a correction factor for allometric $\widehat{M}$ of Kalahari species.

Species Latin name	Species common name	Primary foraging strategy ^a	Allometric scaling rule	Mass (kg) ^c	Allometric $\widehat{M}$ (km)	Empirical $\widehat{M}$ (km) $\pm$ SE (n)	Source of empirical $\widehat{M}$
<i>Taurotragus oryx</i>	Eland	B	Artiodactyla	561	4.64	10.47 $\pm$ 1.40 (12)	Present study
<i>Tragelaphus strepsiceros</i>	Greater kudu	B	Artiodactyla	210	3.60	5.84 $\pm$ 0.71 (18)	Present study
<i>Alcephalus buselaphus caama</i>	Red hartebeest	B	Artiodactyla	161	3.36	5.84 $\pm$ 0.91 (13)	Present study
<i>Antidorcas marsupialis</i>	Springbok	B	Artiodactyla	38	2.31	1.79 $\pm$ 0.15 (13)	Present study
<i>Struthio camelus</i>	Ostrich	B	Artiodactyla	111	3.05	5.16 $\pm$ 1.25 (5)	Present study
<i>Oryx gazelle</i>	Gemsbok	B	Artiodactyla	206	3.58	5.60 $\pm$ 0.58 (17)	Keeping (2014)
<i>Raphicerus campestris</i>	Steenbok	B	Artiodactyla	11.5	1.69	4.50 $\pm$ 0.45 (6)	Keeping (2014)
<i>Connochaetes taurinus</i>	Blue wildebeest	B	Artiodactyla	214	3.62	7.09 ^d $\pm$ 0.12 (9)	Selebatso et al. (2018)
<i>Giraffa giraffa</i>	Giraffe	B	Artiodactyla	1340	5.82	13.70 $\pm$ 1.7 (55)	Brown et al. (2023)
<i>Lycaon pictus</i>	African wild dog	A	Carnivora	27	4.64	24.60 $\pm$ 1.7 (12)	Stander (1998)
<i>Hyaena brunnea</i>	Brown hyena	A	Carnivora	47.5	5.88	31.10 $\pm$ 2.1 (42)	Mills (1990)
<i>Acinonyx jubatus</i>	Cheetah	B	Carnivora	50	6.01	11.44 $\pm$ 0.15 (219)	Keeping et al. (2018)
<i>Panthera pardus</i>	Leopard	A	Carnivora	55	6.26	13.74 $\pm$ 0.81 (16)	Alessandrello (2022)
<i>Panthera leo</i>	Lion	B ^b	Carnivora	178.5	10.27	19.4 $\pm$ 1.4 (16)	Stander (1998)
<i>Crocota</i>	Spotted hyena	A	Carnivora	65	6.72	26.50 $\pm$ 1.7 (140)	Mills (1990)
<i>Proteles cristatus</i>	Aardwolf	B	Carnivora	10	3.05	8.8 $\pm$ 0.5 (12)	Richardson (1987)

<i>Canis mesomelas</i>	Black-backed jackal	A	Carnivora	10	3.05	14.55 ± 2.92 (2)	Kaunda (2001)
<i>Felis silvestris</i>	African wild cat	B	Carnivora	4.75	2.23	5.1 ± 1.18 (8)	Herbst (2009)
<i>Cynictis penicillate</i>	Yellow mongoose	B	Carnivora	0.62	0.95	3.23 ± 0.43 (7)	Cavallini (1993)
<i>Orycteropus afer</i>	Aardvark	B	Carnivora	61	6.54	8.60 ± 1.54 (4)	Keeping (2014)

^aA = Social hunters and scavengers, B = Herbivores and solitary hunters

^bAdult lions mostly hunt alone or in pair in our study area (MPI & LEC, Unpublished data).

^cFollowing the method of Keeping (2014), body masses were taken from Kingdon (1997) for mammals and Hockey et al. (2005) for ostrich. Where ranges were reported, they were calculated by using the mean value of both sexes of the median value for each sex.

^dAlthough Selebatso et al. (2018) present seasonal $\widehat{M}$, the difference between the wet and dry seasons is only 400 meters, which have a negligible impact on the output densities. Therefore, we computed a weighted annual average to avoid introducing a temporal difference for just one species.

SE, Standard error; n, sample size referring to the number of independent data points, i.e. from different individuals or groups. Note that for brown hyena, spotted hyena, and cheetah, n = the number of 24-hour time periods for which animals were followed, likely involving repeated sampling of the same individuals (raw data unavailable).

3. Results

3.1. New empirical $\bar{M}$ for five Kalahari herbivores

A total of 71 trails were collected across all species, at a rate of one or two trails per working day. Following data curation, 10 trails were discarded. As a result, the final dataset includes 61 trails (**Table 4-2**), among which one trail had been extrapolated over one hour, 19 were corrected by removal of observer-induced running portions during the trailing, and 11 had the completion of the 24-hour travel distance estimated by the trackers (see **Appendix 4D**). Removed running portions during the trailing had a median length 198 m and a maximum of 1,215 m, accounting for maximum 7.3 minutes at a conservative running speed of 10km/h, and 2.4 minutes at 30km/h. For trails where the target was re-sighted or just fled upon the observers' approach (50/61), the absolute error around 24 hours is estimated to be at most half an hour. However, of the trails with an error estimated to be over 15 minutes (9/50), all but two were cases where the target had fled after being found resting or foraging slightly earlier than the required time; it is therefore very likely it would have remained in the same place until the required time if it had not detected the observers' presence.

Table 4-2 Average daily travel distance estimates ($\bar{M}$) for each species.

Species	Number of trails (n)	Number of individuals followed per trail	Empirical $\bar{M}$ (km)	Standard error (km)
Eland	12	1-100+	10.468	1.398
Red hartebeest	13	1-12	5.843	0.906
Greater kudu	18	1-12	5.842	0.711
Ostrich	5	2-8	5.155	1.254
Springbok	13	3-43	1.790	0.151

3.2. Temporal stability in daily travel distance

Despite the presence of some variation among the daily travel distance values within each species, no general temporal trend is observed across species (**Figure 4-3** and **Appendix 4E**). Results indicate that ostriches travel greater distances daily as the cold dry season progresses ($\beta_1 = 0.097$, p-value = 0.003, i.e. an increase of 97m per day). However, with only five data points, this could be a spurious effect. Springboks exhibit a nearly significant decrease in daily travel distance over time but its effect size is small ($\beta_1 = -0.013$, p-value = 0.052, i.e. a decrease of 13m per day).

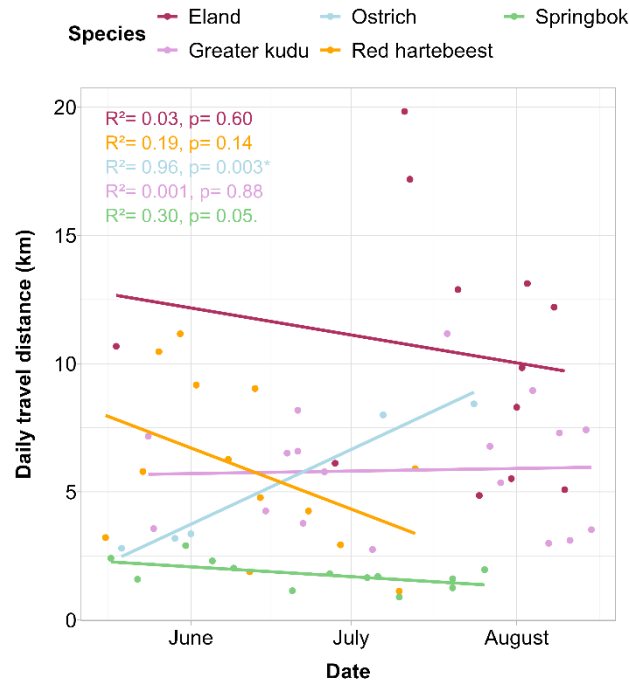


Figure 4-3 Temporal variation in daily travel distance by each species within the cold dry season 2023. Lines are linear regressions applied to each species. R^2 , coefficient of determination; p , p -value of the t -test indicating whether the slope differs from 0; “.” or “*” indicates marginal significance ($p \leq 0.10$) or significance ($p \leq 0.05$).

3.3. Correction coefficient for allometric $\widehat{M}$ of Kalahari species

The model including the allometric $\widehat{M}$ and its interaction with the foraging strategy groups (i.e. Social hunters and scavengers versus Herbivores and solitary hunters) described the data much better than the model assuming both groups share the same regression line (**Table 4-3**). For species in both groups, empirical $\widehat{M}$ is predicted to be significantly higher than allometric $\widehat{M}$, although this effect is greater for social hunters and scavengers (**Figure 4-4** and **Appendix 4E**). With an adjusted R^2 of 0.97, the model shows a high level of predictive accuracy. Removing the lion (*Panthera leo*) or black-backed jackal (*Canis mesomelas*) data point for their potentially high leverage on the model’s parameters inflicts only a negligible change to the estimated values of the

regression slopes (+0.012 and -0.006 respectively). Springbok is the only species whose empirical $\widehat{M}$ (1.79 km) is smaller than its allometric $\widehat{M}$ (2.31 km), likely because springboks rarely leave pans in the cold dry season (Moatswi, 2019). Similarly, removing the springbok data point has minimal impact on the slope for its group (+0.017). Finally, ostrich falls almost perfectly on the regression line despite not being an Artiodactyla. This supports our decision to group it with Artiodactyla and attests to the reliability of its empirical $\widehat{M}$, despite the small sample size (n=5). Therefore, we suggest two coefficients to correct allometric $\widehat{M}$ of Kalahari species subject to the Artiodactyla and Carnivore scaling rules: $\beta_1 = 4.698 \pm 0.370$ (SE) for social hunters and scavengers and $\beta_1 = 1.917 \pm 0.097$ (SE) for herbivores and solitary hunters.

Table 4-3 AICc-based model selection for linear regression of empirical $\widehat{M}$ against allometric $\widehat{M}$ and foraging strategy.

^a Model	^b K	LL	AICc	Delta_ AICc	AICc Wt
Allometric + Allometric * Foraging strategy	3	-44.09	95.68	0.00	1.00
Allometric	2	-64.64	133.99	38.31	0.00
Null	2	-70.04	144.79	49.12	0.00

^a Since the intercept is fixed at zero, the 'Foraging strategy' variable does not exist as a main effect.

^bK, number of model parameters; LL, log-likelihood; AICc, Akaike Information Criterion corrected for small sample sizes; Delta_AICc, difference in AICc between the current model and the best model; AICcWt, Akaike weight.

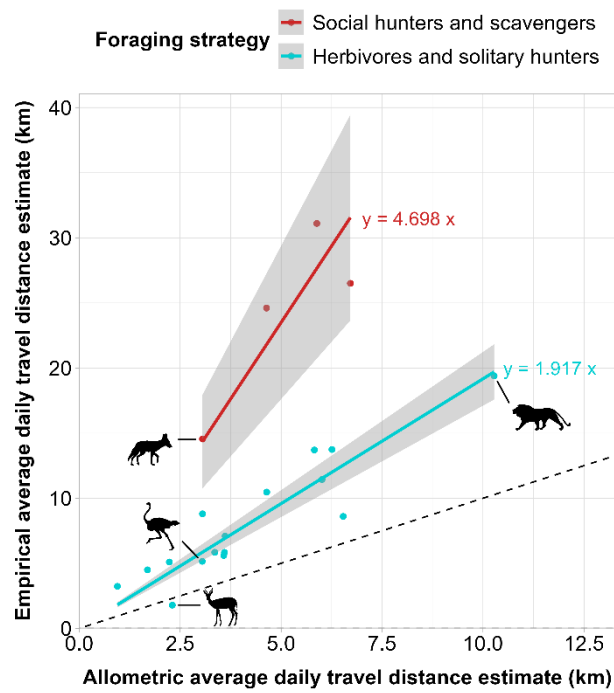


Figure 4-4 Computation of empirical $\widehat{M}$ as a simple linear function of allometric $\widehat{M}$ for the two foraging strategy groups, with a 95% confidence interval (in grey).

The black dashed line represents the scenario where empirical $\widehat{M}$ and allometric $\widehat{M}$ are equal ($\beta_1 = 1$). The data points for springbok, ostrich, lion, and black-backed jackal, whose peculiarities are detailed in the main text, are indicated by species-specific icons.

Icon sources: Springbok by Robert Hering from Phylopic ([CC BY 3.0](https://commons.wikimedia.org/wiki/File:Springbok.jpg)); ostrich, lion and black-backed jackal from Phylopic ([PDM 1.0](https://commons.wikimedia.org/wiki/File:Ostrich.jpg)).

3.4. Case study: population density estimates from track counts in Khutse Game Reserve and southern Central Kalahari Game Reserve

Figure 4-5 summarises population density estimates obtained from track surveys, calculated via the FMP formula with $\hat{p}_2$ assumed to be 1. We used the newly acquired empirical $\widehat{M}$ from **Table 4-2** for the five species we trailed, allometric $\widehat{M}$ corrected with the ‘herbivores and solitary hunters’ coefficient (1.917) for duiker (*Sylvicapra grimmia*) and warthog (*Phacochoerus africanus*), and existing empirical $\widehat{M}$ from **Table 4-1** for the other species. Small antelopes, i.e. steenbok (*Raphicerus campestris*) and duiker, are the most abundant, along with gemsbok (*Oryx gazella*), known for being the most arid-adapted large antelope (Knight, 1991; van der Walt et al., 1984). In contrast, blue wildebeest (*Connochaetes taurinus*) and springbok are notably few, reflecting their significant population declines in recent decades (DHV, 1980; DWNP, 2015; Thouless, 1998). Overall, dry season densities tend to be systematically lower for all species, compared with the wet season.

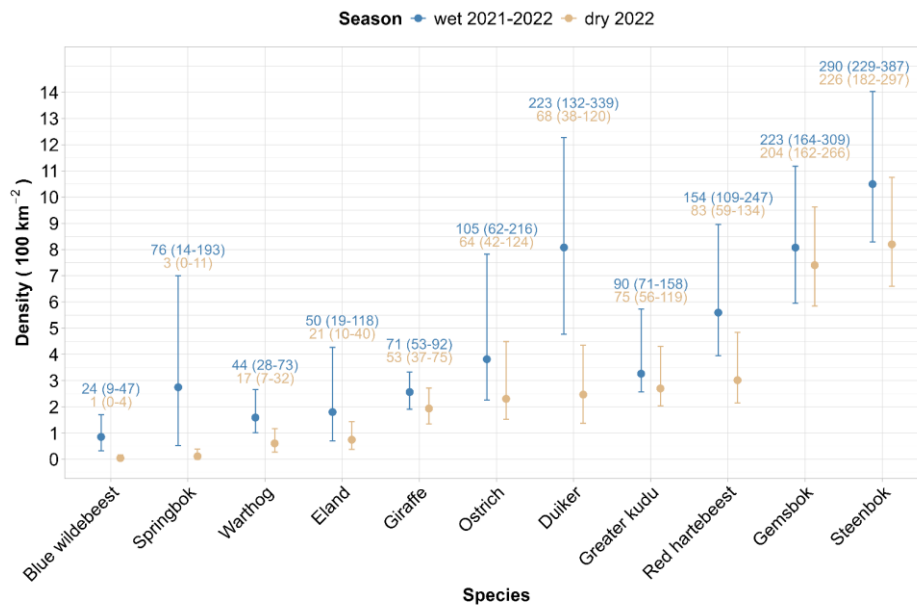


Figure 4-5 Population density estimates per species per season in KGR and southern CKGR, Botswana.

On top of the error bars are indicated the species abundance estimates $\pm$ 95% bias-corrected and accelerated confidence intervals, calculated for the track survey study area of 2761.56km².

4. Discussion

The sandy regions of southern Africa, similarly to other ecosystems with a soft substrate, are particularly well suited for track-based techniques to monitor wildlife populations. Consequently, they have drawn the attention of practitioners (Ahlsweide et al., 2019; Funston et al., 2010; Keeping, 2014; Midlane et al., 2014; Winterbach et al., 2016). Like any technique track surveys present some limitations and challenges (Dröge et al., 2020; Hayward et al., 2015; Karanth et al., 2003), however, they often provide the best cost-benefit approach. A promising method to alleviate some of these challenges is the FMP formula, an absolute density estimator based on track counts along transects that integrates animal detectability ($\hat{p}_1$). Our study offers several new elements to enhance the accuracy of the species' average daily travel distance estimate ($\hat{M}$) that serves as a pivotal parameter in the FMP, enabling an accurate conversion of the 'number of tracks' into the 'number of animals'. We also demonstrate the potential and value of research and conservation projects designed in collaboration with local communities.

4.1. Wildlife trailing as a reliable method to collect species daily travel distances inclusively of Indigenous knowledge

With 61 exploitable independent trails recorded in 75 days of work (including spotting days), we confirmed that our forward trailing protocol can capture very detailed movements of large herbivores over a precise 24h period. GPS tagging, while renowned for its extensive data collection on animal movements (Kays et al., 2015), is often limited by the number of individuals that can be studied and effectively captured, potentially leading to unrepresentative samples due to intraspecific variability in movement behaviours (Hebblewhite & Haydon, 2010; Hertel et al., 2020). Trailing, in contrast, offers higher control and adaptability in data collection, non-invasively and likely at a lower cost (approximately 110 USD per trailing, in case of vehicle renting). It allows for (1) collecting data on more independent individuals or groups, only biased by those that are visible, largely improving the generality of movement estimates, (2) easily spreading trailing efforts across space or time as needed, while (3) providing an opportunity to involve and value Indigenous knowledge. Animal trailing also allows for the collection of detailed information beyond distance travelled, such as movement tortuosity in relation to resources or threats at very fine spatial scale (e.g. in Whittington et al. (2004)). Trackers in this study also demonstrated an impressive ability to accurately interpret the target's behaviour along the trails, reconstructing activities such as resting, foraging, lying down, trotting, running, fighting, digging, mating, or rubbing against a

tree. Similar skills have also been documented by Stander et al. (1997) among Namibian Kalahari San trackers. Such data are still challenging to obtain by other means at comparable resolution, except by visually following habituated animals (Cavallini, 1993; Mills, 1990), which risks occasionally altering their natural behaviour. These behavioural data can be correlated with various environmental variables at fine spatial and, to a lesser extent, temporal scales to understand what animals are doing where, when, why and how (Murray et al., 1995; Stander, 1994; Subach et al., 2022).

Yet, trailing does require a fine estimation of the trail's freshness for continuously adjusting the trailing pace, in order to meet the target at the required time. Highly skilled trackers and former traditional hunters are quite capable to approach the target animal without being detected. So that even a target re-sighted too early can be observed from a distance until the required time. To the extent possible, we also advise creating a re-sighting time buffer by spotting animals when they are likely resting (midday to afternoon), observing them for up to an hour without disturbance, and recording their location every five minutes if they move. Errors surrounding the 24-hour distance calculation are nonetheless possible, whether from estimating the trail's end, extrapolating incomplete trails, or removing observer-induced running portions. However, we believe these errors to be generally minimal following our trail curation protocol (see **Appendix 4D**). Moreover, these errors are likely much smaller than those associated with target selection, considering the substantial intraspecific variance in daily travel distances collected.

Although effective for large to medium-size herbivores, our trailing method might need adjustment to accommodate various species ecologies. Unlike antelopes, ostriches have soft feet, so only their nails leave marks on harder terrain. Combined with their long stride, this makes ostriches particularly difficult to trail, which explains our smaller sample size for this species (n=5). To increase the chances of successfully completing trails, slightly humid soil can be advantageous, and practitioners should avoid spotting single animals around large pans, especially in the dry season. Smaller diel animals may present a home range size too small to forward trail them without systematically impacting their movement. In such a case, Keeping and Pelletier (2014) effectively collected daily travel distance of steenboks by spotting animals 24 hours after rainfall. From there, the animal was back trailed to the point where the tracks became marked by raindrops. However, this approach can only be applied to abundant and readily visible species (for precisely timing initial spotting), and limits trailing to the wet season only. For some nocturnal species hiding underground during the day,

their burrows can be used as a starting point to back or forward trail their movements of the previous night, as done with aardvark (Keeping, 2014). Other innovative solutions have been explored, such as using fluorescent powder detectable by ultraviolet light for trailing reptile and small mammals, although generally reliable for small-scale movements only (Brehme et al., 2013; Furman et al., 2011). In low density environments, camera traps can be placed at animal activity hotspots to increase the chance of spotting potential targets on day 1; photographs are then reviewed in the evening for any sightings around midday and afternoon hours acting as a substitute of the initial live spotting of the animal. For particularly rare or elusive species, GPS tagging using high frequency fixes might still be the most effective method for collecting daily travel distances. The limitations of calculating straight-line distances between GPS points can now be addressed using a recently developed estimator known as continuous-time speed and distance (CTSD) (Noonan et al., 2019). If fix frequency is low (as infrequent as one fix per 24 hours), it can still be used to guide back trailing of individuals, a technique that can also prove useful for potentially dangerous animals.

4.2. Accurate estimates of daily travel distance are key for reliable FMP-derived density estimates, but survey design is equally important

The accuracy of $\widehat{M}$ depends on both the time and space dimensions. Spatially-speaking, $\widehat{M}$ should ideally be estimated within the study area where the track survey is conducted, and concurrently with the survey. However, this is often not feasible due to logistical or resource constraints. Therefore, when selecting an existing empirical $\widehat{M}$ for use in the FMP equation, it is essential to ensure it was estimated in an area ecologically similar to the study area. Accessing relevant data has now become more convenient with the growing availability of open source databases (e.g. **Table 4-1** and Ahlswede et al. (2019) for the Kalahari; [Movebank](#) worldwide). When empirical $\widehat{M}$ are not available, we showed that allometrically-derived estimates can be reliable approximations, provided they have been calibrated to the region and, ideally, to the species ecology. We found, unsurprisingly, that allometric $\widehat{M}$ of social hunters and scavengers require a correction coefficient nearly 2.5 times greater than those of herbivores and solitary hunters. For instance, brown hyenas (*Hyaena brunnea*) and black-backed jackals primarily scavenge and opportunistically hunt small, sparsely distributed food items. This requires extensive travel relative to their body mass to meet daily subsistence needs in the Kalahari (Kaunda, 1998; Mills, 1990; Owens & Owens, 1978). On the other hand, African wild dogs (*Lycaon pictus*) routinely commute in packs, flushing out prey, then engaging in

multiple opportunistic cursorial chases (Hubel et al., 2016). While their food acquisition strategy likely has an important aspect of their wide-ranging behaviour, avoiding inter-specific competition with apex predators is also believed to contribute to it (Jordan et al., 2023). In contrast, felids scavenge much less and rather invest significant time in stalking or ambushing their prey (Bothma & Walker, 1999). As a result, they do not cover as much distances while foraging.

Temporally-speaking, the accuracy of $\widehat{M}$ may also be enhanced if it represents a time period ecologically equivalent to the survey period. The data from our study area illustrate that travelled distances vary from day to day for a given species, most probably due to multiple factors. However, it is reasonable to assume they converge to a more stable average over similar environmental conditions, likely linked to temporality such as seasons (Stephens et al., 2006). Hence, we found that species-specific $\widehat{M}$ remain essentially stable within the cold dry season (May-August), making them valid for this period but potentially not beyond; between-season differences still need more investigation. As the dry season progresses, the food and moisture availability decreases, which may force animals to move on average further daily in order to meet their resource needs (Owen-Smith & Cain, 2007; Owen-Smith & Goodall, 2014). For instance, Deacon (2015) demonstrated that female Kalahari giraffe (*Giraffa giraffa*) travelled distances 13% longer during the dry season compared with the wet season. Cooler dry season months (May to August) may also favour more movements during midday hours when animals would usually rest during the hotter months of the year (Berry et al., 2023; Boyers et al., 2019). In this context, Selebatso et al. (2018) found that Kalahari blue wildebeest travelled on average 745 m/24h more in cool months (cold dry season) compared with hot months (wet and hot dry season), based on hourly GPS telemetry data. However, we may expect variations according to the species ecology. As Owen-Smith & Cain (2007) noted: “[...] grazers like white rhino (*Ceratotherium simum*; Owen-Smith (1988)) and African buffalo (*Syncerus caffer*; Ryan et al. (2006)) expand their home ranges during the dry season seeking areas where grass still remains green, while browsers like black rhino (*Diceros bicornis*; Goddard (1967)) and kudu (*Tragelaphus strepsiceros*; Owen-Smith (1979)) expand their ranges during the wet season to exploit the herbaceous ‘forbs’ that become temporarily available at this time”. In our study, this may apply to the duiker (browser and frugivore (Wilson, 2013)), which shows density estimates three times higher in the wet season than in the dry season. The unexpected amplitude of the variation suggests a differential $\widehat{M}$ between seasons, likely with a higher value in the wet season compared with the dry season. Moatswi (2019) also found that springbok avoided off-pan habitats during the cold dry

season in the Kalahari and show a slight tendency to decrease their movements from the cold dry to the hot dry season, possibly to conserve water and energy. This is consistent with our observations. He also reported slightly higher daily travel distances during the wet season, likely due to increased movement between pans to meet the elevated nutritional requirements of lactating females and growing calves.

Depending on how large temporal variations in $\widehat{M}$ might be, practitioners must decide if the efforts to obtain time-specific $\widehat{M}$ are justified relative to the desired accuracy of population density estimates. To serve in a monitoring situation, the variation in detectability (here driven by $\widehat{M}$ where survey design and protocol remain constant) does not have to be null, just substantially less than the variation in population size sought to be detected (Johnson, 2008). Hence, although using the same $\widehat{M}$ when calculating densities for the wet and dry season for each species, we still observed that dry season abundance tends to be systematically lower than wet season abundance. This seasonal fluctuation is supported by various studies (Bergström & Skarpe, 1999; Ngwamotsoko, 1985); Kalahari populations typically decline during the dry season when death rates are not offset by births and may even rise due to food and water scarcity. Some species, such as blue wildebeest, may also display seasonal movements to the edges of the Kalahari, which provide better conditions during the dry season (Bonifica, 1992; Verlinden, 1998). If dry season $\widehat{M}$ exceeds wet season $\widehat{M}$, then our observed seasonal difference in abundance would be even more marked. The opposite is also possible, although unlikely to the point of inverting the wet versus dry season tendency in abundance. Therefore, given our approach already detected the expected seasonal difference in $\widehat{D}$, the average seasonal difference in $\widehat{M}$ is probably limited and unlikely to exceed the magnitude of the seasonal variation in population size. However, differential $\widehat{M}$ should not be dismissed immediately (e.g. duiker in **Figure 4-5**) and must be considered if track surveys are performed during specific time periods, particularly when the species of interest exhibits seasonal movement or migratory patterns (Owen - Smith et al., 2020; Selebatso, Bennitt, et al., 2018; Zidon et al., 2017).

Finally, in terms of species absolute abundance, a couple of discrepancies with independent knowledge from our study area are worth pointing out. Springboks are estimated at 3 individuals in the dry season over the entire study area, while we are aware of at least 3 or 4 herds simultaneously present. This means that our track survey transect design does not survey variations in local densities of springbok in proportion. This is because transects go around rather than through pans, which are springbok primary habitats from

where they rarely move out, especially in the dry season (Moatswi, 2019). Elands are sometimes seen in large herds north of the study area, with occasional commutes to its north-western section, possibly resulting in underestimated density due to limited transect coverage in that area. Therefore, adequate transect design and survey effort are also essential to return accurate and precise density estimates (Keeping & Pelletier, 2014; Stephens et al., 2006).

5. Conclusions

The interpretation of animal tracks and signs is one of the oldest human practices (Liebenberg, 1990b). Alongside visually following habituated animals, these methods were common tools in wildlife studies worldwide during the last century (Formozov, 1932; Kurki et al., 1998; Soutiere, 1979; Stander, 1994; Stoltz & Saayman, 1970). More recently, they have been increasingly replaced by new technologies, which reduce field time while collecting large amounts of data simultaneously at landscape scale (Kays et al., 2015; Trollet et al., 2014). While undoubtedly revolutionary to answer some research questions, new technologies can still rarely acquire the wealth of detailed information provided by traditional field observations. Moreover, they often trade the quantification of population biological variation for a very detailed measure of a few individuals (Hebblewhite & Haydon, 2010). Rather than being exclusive, both approaches are increasingly recognised as complementary. Therefore, there are growing calls to merge Indigenous knowledge with modern methods in conservation and wildlife research (Dorfman et al., 2023; Finerty et al., 2024; Liebenberg et al., 2017). Moreover, conservation can be challenging where local inhabitants bear high costs of living alongside wildlife (Allendorf, 2022; Barrow & Fabricius, 2002). Involving local community members in collaborative projects can create mutual value, reinforcing cultural identity and empowerment over resource management, formally recognizing their knowledge, and providing employment opportunities and new experiences (Finerty et al., 2024; Gielen et al., 2024; Lilleyman et al., 2022). In particular, track-based work can be applied in various ecosystems where suitable substrate (e.g. snow, dust, sand, mud) and tracking skills exist (Brandišauskas, 2016; Ens et al., 2015; Esbach, 2023). We believe that such participatory approaches can improve attitudes towards wildlife, fostering human-wildlife coexistence and enhancing conservation outcomes. Furthermore, beyond knowledge acquisition, humanity would greatly benefit from a genuine reconnection with the rest of nature, something that the traditional ways can profoundly impart.

Supplementary material

An extended derivation of the Formozov-Pereleshin-Malyshev formula in relation to detectability (**Appendix 4A**), the forward trailing field protocol (**Appendix 4B**), the CyberTracker application for animal trailing (**Appendix 4C**), the curation of trailing data (**Appendix 4D**), and additional detailed statistical outputs (**Appendix 4E**) are available in the **Supplementary Material**.

