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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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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 ($\widehat{M}$). Its main limitation lies in accurately estimating $\widehat{M}$ relevant to the survey's specific time period and location. If empirical $\widehat{M}$ from the study region is not available, $\widehat{M}$ can be estimated allometrically, but less accurately, through body mass-$\widehat{M}$ scaling rules. This study aims to improve the accuracy of FMP-derived density estimates by refining both empirical and allometric $\widehat{M}$ estimations.

Methods We tested a cost-effective forward trailing technique to collect high-quality empirical $\widehat{M}$ for large herbivore species with local certified trackers, in Khutse Game Reserve and Central Kalahari Game Reserve, Botswana. Since allometric $\widehat{M}$ values are underestimated in the Kalahari, we calibrated them using empirical $\widehat{M}$ from this study and the literature. Finally, we integrated our findings to estimate densities of 11 herbivore species using track surveys and the FMP formula.

Results Through trailing, we provided empirical $\widehat{M}$ for five herbivore species, which previously lacked data for the area, and confirmed the temporal stability of daily travel distance values within the study season. We derived two separate coefficients to directly correct allometric $\widehat{M}$ for Kalahari species based on their foraging strategies. Based on our interpretation of the animal density estimates obtained via the FPM, we discuss the importance of the accuracy of $\widehat{M}$, transect design, and survey effort for population monitoring.

Conclusion Our research demonstrates the effectiveness of the forward trailing technique for accurately estimating $\widehat{M}$ of large herbivores in sandy substrates. It also provides coefficients to directly correct allometric $\widehat{M}$ for Kalahari species and delivers density estimates for multiple herbivores species across 2800 km^2 of protected areas. These new

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elements strengthen the use of track data for wildlife monitoring in low-density environments, although we encourage further research to assess the need of time-specific $\widehat{M}$. 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, CyberTracker

Background

Conservation of natural ecosystems is currently a global priority, as the Earth is facing an unprecedented environmental crisis [1, 2]. 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 [3, 4]. As counting all individuals of a population is rarely achievable, practitioners rely on estimations [5, 6]. 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 [7–9].

Animal track surveys are one of the techniques relying on indirect observations. Here, we define track surveys as the detection, geo-location, species identification and count of animal tracks (i.e. footprints) that intersect transects within the study area [10–12]. 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 [10, 13, 14]. They also return higher encounter rates per sampling effort at a lower cost [7, 15–17]. 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 [18–21].

Track surveys have been used in the snowy regions of Russia for nearly a century [22–26], notably by applying the Formozov–Malyshev–Pereleshin (FMP) formula to estimate true population density. Since the early twenty-first century, the FMP formula has been increasingly applied in diverse environments, including the sandy Kalahari [10, 13], mud and clay soils [16] or snow [27] in Europe, and tropical forests [28]. The FMP formula 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:

$$\hat{D} = \frac{\pi}{2} \cdot \frac{\hat{x}}{S \cdot \widehat{M}} \tag{1}$$

where, for a given species, estimated counts of fresh (≤24 h old) tracks ($\widehat{x}$) along linear transects of total length S (i.e. track index $\frac{\widehat{x}}{S}$) are converted into population density estimates ($\widehat{D}$) using the average estimated distance animals travel in 24 h ($\widehat{M}$). To obtain population abundance, $\widehat{D}$ 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 $\widehat{M}$, as a species travelling longer distances daily should intersect transects more often than a sedentary species. Therefore, $\widehat{D}$ is proportional to $\frac{\widehat{x}}{S}$ and also inversely proportional to $\widehat{M}$. To qualify as an absolute estimate, $\widehat{D}$ must also account for track detectability, which consists of two components: the probability $\widehat{p_1}$ that an animal movement path intersects with the total transect length at least once, so that tracks are left to be recorded, and the probability of track detection $\widehat{p_2}$ by the observers [29]. Due to the difficulty in measuring $\widehat{p_1}$, track counts have most often been used as indices of relative abundance [15, 30–32]. Converting them to absolute population estimates typically requires individual animal recognition [33–36], calibration to true abundance [12, 37], or specialised modelling [38]. While effective in specific contexts, these methods often lack broad applicability or still face issues regarding detectability or density estimate precision [39–41]. In contrast, the FMP formula inherently accounts for $\widehat{p_1}$ through all its parameters, provided all tracks are recorded regardless of individuals' identity. Then, $\widehat{p_2}$ can either be measured to directly correct the observed track count, or assumed close enough to 1 (more details on detectability under the FMP formula provided in Additional file 1).

While $\widehat{x}$ and S are directly recorded during the track survey, $\widehat{M}$ is not. Obtaining quality $\widehat{M}$ relevant to the survey's location and time period of the year is currently the main practical limitation to the FMP approach. Empirical $\widehat{M}$ 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 [42–44]. 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) [45]. Furthermore, it may underestimate $\widehat{M}$ if GPS fix frequency is too low [46, 47]. Alternatively, $\widehat{M}$ can be obtained by visually following habituated animals [48, 49], or via thread trailing [50]. These techniques provide much finer-scale estimates but are limited to a few specific populations. In areas with suitable substrate, high-resolution $\widehat{M}$ 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 [51–53] or backward using recent rain [51] or snow falls (as performed by [36]); 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 [7]. Beyond wildlife population monitoring [13, 54, 55], FMP-based track survey data recently supported a comprehensive wildlife habitat and connectivity analysis [56, 57], informing a government-commissioned land-use plan for 220,000km^2 of Botswana's Kalahari region [58]. However, despite this increased use, a limitation remains: trustworthy empirical $\widehat{M}$ are currently available for a limited number of species only [10, 13]. For other species, $\widehat{M}$ is calculated allometrically through a scaling rule with the species' body mass [59]. However, this approach tends to underestimate $\widehat{M}$ for Kalahari species, resulting in an overestimation of $\widehat{D}$; a bias currently requiring $\widehat{D}$ to be corrected by a unique coefficient developed by Keeping et al. [10]. However, we argue that certain species groups may travel greater distances daily (i.e. requiring different correction coefficients) depending on the specificities of their ecologies.

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 ($\widehat{M}$) to enhance the accuracy of animal density ($\widehat{D}$)? 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 $\widehat{M}$ 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 $\widehat{M}$ of Kalahari mammal species to derive new coefficients for directly adjusting allometrically-derived $\widehat{M}$, 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.

Methods

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 3900km^2 and 2800km^2 respectively, located between 23°–24°S and 024°–025°E (Fig. 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 [60, 61]. Annual rainfall averages 400 mm [62], occurring almost exclusively during the rainy season between November to April [63]. Isolated clay depressions known as pans are the only source of surface water after rains, and such free water is highly ephemeral [64]. 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 [65, 66]. 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 gaps along its length [67]. Large herbivore species often exhibit seasonal movements between resource areas, which can vary spatially in response to localised rainfall. The road network is sparse, with 550 km of sand roads used by tourists and park management officials.

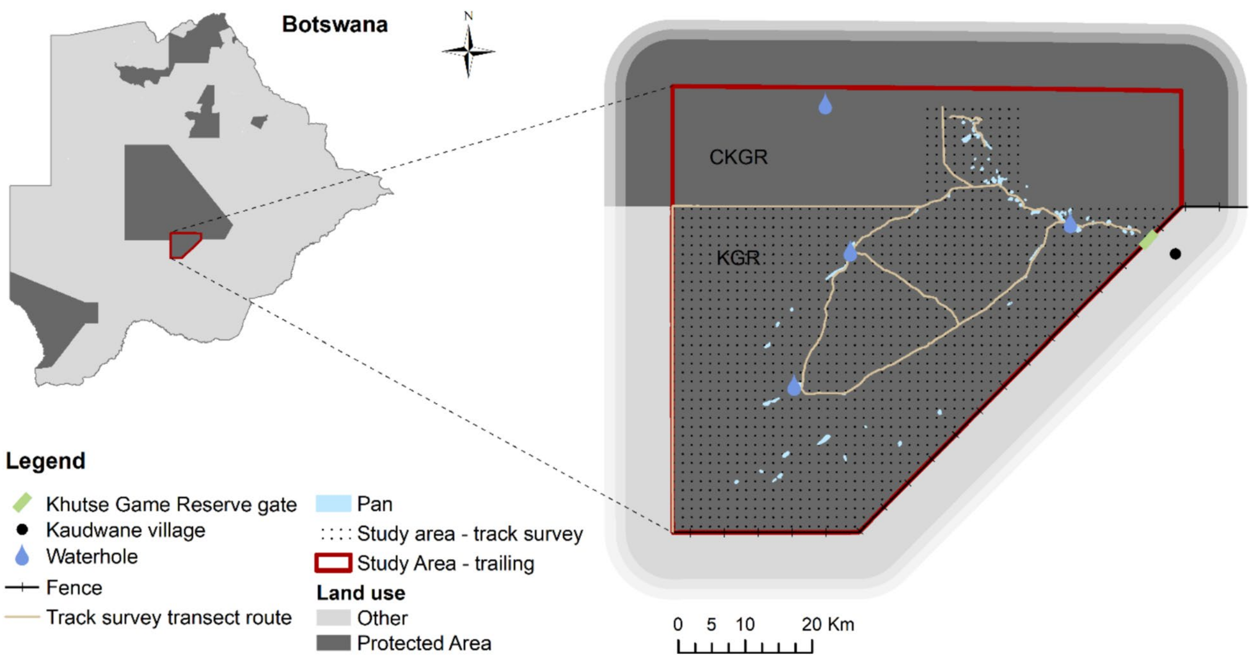

Fig. 1 The trailing study area comprises Khutse Game Reserve (KGR) and a southern portion of the Central Kalahari Game Reserve (CKGR), both protected areas situated in the Kalahari Desert, Botswana. Track surveys were conducted within KGR and a small portion of CKGR, where they sample 59% of the existing sand roads

Forward trailing protocol and calculation of empirical $\widehat{M}$

We collected daily travel distances for five large and medium-size Kalahari herbivore species that are key to protected area management and still lacked empirical $\widehat{M}$: eland (*Taurotragus oryx*), red hartebeest (*Alcephalus buselaphus caama*), greater kudu (*Tragelaphus strepsiceros*), springbok (*Antidorcas marsupialis*), and ostrich (*Struthio camelus*). All species typically occur in herds or family groups within the study area, often large for eland and springbok. However, group sizes usually decline in the dry season, when males are also more frequently solitary. To ensure data of high spatial resolution, we developed a two-day forward trailing approach—adapted from techniques tested in both snow [53] and sand [51]—in consultation with local expert trackers based on their knowledge of animal behaviour (Fig. 2). This method is supported by a detailed, replicable field protocol for accurately estimating daily travel distances, described in full in Additional file 2. In short, 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,

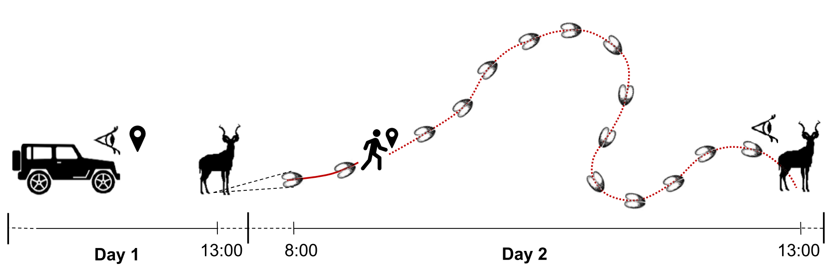

Fig. 2 Illustration of the forward trailing method we developed to collect species 24-h travel distances. On the first day, the animal(s) is spotted at a given time and location. On the second day, the same animal(s) is trailed forward (red line) from the location it was spotted on day 1, until observers 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), Jeep by Isaac haq from Noun project (CC BY 3.0), Eye by dh park from Noun project (CC BY 3.0), person and pin from Microsoft Corporation 2019, greater kudu track from Liebenberg [117]

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 h 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 s. 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-h trail. If the target was not met on time, trailing was pursued when possible, until trackers estimated that 24 h of travel distance had been sampled based on the trail's freshness. A description of our CyberTracker application is available in Additional file 3.

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 [68]). 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 h, (2) observer-induced behaviour in the target, and (3) estimating the completion of the 24-h 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 Additional file 4 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.

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.

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

To improve allometrically-derived $\widehat{M}$, we revisited the correction approach proposed by Keeping et al. [10], exploring coefficients that directly adjust $\widehat{M}$, rather than $\widehat{D}$, based on a larger empirical dataset. To do so, we extended the dataset of empirical $\widehat{M}$ collected for the five species in this study with existing data for other Kalahari species, totalling 9 Artiodactyla and 11 Carnivora species (Table 1). 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, see Table 1 for sources), emulated using data from a variety of species across different biomes (see Supplementary Material of [59]):

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

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 [59]. 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 [59, 69–71]. 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 [49, 71], versus other strategies such as herbivores and solitary hunters (group B) (Table 1). Three linear regression models were compared using model selection based on the Akaike Information Criterion corrected for small sample sizes (AICc)

Table 1 Dataset of species-specific empirical $\widehat{M}$ and allometric $\widehat{M}$ used to generate correction coefficients 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) ± SE (n)	Data collection method for empirical $\widehat{M}$ [d]	Source of empirical $\widehat{M}$
Taurotragus oryx	Eland	B	Artiodactyla	561	4.64	10.47 ± 1.40 (12)	Trailing	Present study
Tragelaphus strepsiceros	Greater kudu	B	Artiodactyla	210	3.60	5.84 ± 0.71 (18)	Trailing	Present study
Alcephalus buselaphus caama	Red hartebeest	B	Artiodactyla	161	3.36	5.84 ± 0.91 (13)	Trailing	Present study
Antidorcas marsupialis	Springbok	B	Artiodactyla	38	2.31	1.79 ± 0.15 (13)	Trailing	Present study
Struthio camelus	Ostrich	B	Artiodactyla	111	3.05	5.16 ± 1.25 (5)	Trailing	Present study
Oryx gazella	Gemsbok	B	Artiodactyla	206	3.58	5.60 ± 0.58 (17)	Trailing	[10]
Raphicerus campestris	Steenbok	B	Artiodactyla	11.5	1.69	4.50 ± 0.45 (6)	Trailing	[10]
Connochaetes taurinus	Blue wildebeest	B	Artiodactyla	214	3.62	7.09 ± 0.12 (9)	GPS-tagging	[99]
Giraffa giraffa	Giraffe	B	Artiodactyla	1340	5.82	13.70 ± 1.7 (55)	GPS-tagging	[118]
Lycaon pictus	African wild dog	A	Carnivora	27	4.64	24.60 ± 1.7 (12)	Following habituated animals	[42]
Hyaena brunnea	Brown hyena	A	Carnivora	47.5	5.88	31.10 ± 2.1 (42)	Following habituated animals	[49]
Acinonyx jubatus	Cheetah	B	Carnivora	50	6.01	11.44 ± 0.15 (219)	Following habituated animals	[7, 55]
Panthera pardus	Leopard	A	Carnivora	55	6.26	13.74 ± 0.81 (16)	GPS-tagging	[119]
Panthera leo	Lion	B[b]	Carnivora	178.5	10.27	19.4 ± 1.4 (16)	Following habituated animals	[42]
Crocuta crocuta	Spotted hyena	A	Carnivora	65	6.72	26.50 ± 1.7 (140)	Following habituated animals	[49]
Proteles cristatus	Aardwolf	B	Carnivora	10	3.05	8.8 ± 0.5 (12)	Following habituated animals	[120]
Canis mesomelas	Black-backed jackal	A	Carnivora	10	3.05	14.55 ± 2.92 (2)	Radio-tracking	[121]
Felis silvestris	African wild cat	B	Carnivora	4.75	2.23	5.1 ± 1.18 (8)	Following habituated animals	[122]
Cynictis penicillate	Yellow mongoose	B	Carnivora	0.62	0.95	3.23 ± 0.43 (7)	Radio-tracking	[84]
Orycteropus afer	Aardvark	B	Carnivora	61	6.54	8.60 ± 1.54 (4)	Trailing	[10]

[a] A = Social hunters and scavengers, B = Herbivores and solitary hunters

[b] Adult lions mostly hunt alone or in pair in our study area (Max Planck Institute & Leopard Ecology & Conservation, unpublished data)

[c] Following the method of [10], body masses were taken from [123] for mammals and [124] for ostrich. Where ranges were reported, they were calculated by using the mean value of both sexes of the median value for each sex

[d] Only species with high-quality empirical $\widehat{M}$ were included. For giraffe and leopard, hourly GPS fixes were analysed using continuous-time movement models (ctmms). For black-backed jackal and blue wildebeest (1-h fixes), and yellow mongoose (15-min fixes), straight-line distances were used, likely causing only a small underestimation of $\widehat{M}$: jackals move along fairly straight paths [125], wildebeest are highly nomadic (assumed low tortuosity) with a large dataset, and mongoose data were high-frequency

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-h time periods for which animals were followed, likely involving repeated sampling of the same individuals (raw data unavailable)

(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.

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 [29], was executed by a single survey team and refined to maximise the probability of detecting existing tracks ($\widehat{p_2}$), which is 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 ± SD Track & Sign score of 98.0 ± 1.75% by CyberTracker Conservation's Tracker Certification System [68]. 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 h preceding the survey. Upon detection, animal tracks from the previous 24 h 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 [72] (see steps in [10]), using R (version 4.3.2). In this process, each transect within each season was treated as independent even if repeatedly sampled each month.

Results

New empirical $\widehat{M}$ 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 due to biases that could not be corrected (see Additional file 4 for details). As a result, the final dataset included 61 trails (Table 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-h travel distance estimated by the trackers (see Additional file 4). Removed running portions during the trailing had a median length of 198 m and a maximum of 1,215 m, accounting for maximum 7.3 min at a conservative running speed of 10 km/h, and 2.4 min at 30 km/h. For trails where the target was re-sighted or just fled upon the observers' approach (50/61), the absolute error around 24 h was estimated to be at most half an hour. However, of the trails with an error estimated to be over 15 min (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.

Temporal stability in daily travel distance

Despite the presence of some variation among the daily travel distance values within each species, no general

Table 2 Average daily travel distance estimates ($\widehat{M}$) for each species

Species	Number of trails (n)	Number of individuals followed per trail	Empirical $\widehat{M}$ (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

temporal trend was observed across species (Fig. 3 and Additional file 5). Results indicated that ostriches travelled greater distances daily as the cold dry season progresses (β1 = 0.097, p-value = 0.003, i.e. an increase of 97 m per day). However, with only five data points, this could be a spurious effect. Springboks exhibited a nearly significant decrease in daily travel distance over time but its effect size was small (β1 = -0.013, p-value = 0.052, i.e. a decrease of 13 m per day).

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 3). For species in both groups, empirical $\widehat{M}$ was predicted to be significantly higher than allometric $\widehat{M}$, although this effect was greater for social hunters and scavengers (Fig. 4 and Additional file 5). With an adjusted R^2 of 0.97, the model showed 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 inflicted only a negligible change to the estimated values of the regression slopes (+0.012 and − 0.006 respectively). Removing blue wildebeest (*Connochaetes taurinus*) due to potential underestimation of their empirical $\widehat{M}$ (see footnote "d" in Table 1) also results in a minimal change in slope (-0.002). Springbok was the only species whose empirical $\widehat{M}$ (1.79 km) was smaller than its allometric $\widehat{M}$ (2.31 km), likely because springboks rarely leave pans in the cold dry season [73]. Similarly, removing the springbok data point had minimal impact on the slope for its group (+0.017). Finally, ostrich fell 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 3 AICc-based model selection for linear regression of empirical $\widehat{M}$ against allometric $\widehat{M}$ and foraging strategy

Model[a]	K[b]	LL	AICc	Delta_AICc	AICcWt
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

[b] K, 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

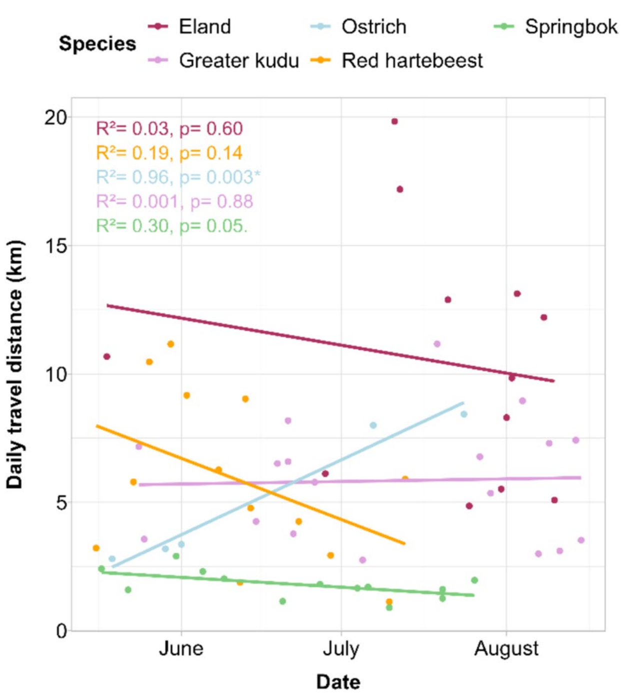

Fig. 3 Temporal variation in daily travel distance by each species within the cold dry season 2023. Lines are linear regressions applied to each species. R^2, coefficient of determination; *p*, *p*-value of the t-test indicating whether the slope differs from 0; "." or "*" indicates marginal significance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

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

Figure 5 summarises population density estimates obtained from track surveys, calculated via the FMP formula with $\widehat{p}_2$ assumed to be 1. We used the newly acquired empirical $\widehat{M}$ from Table 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 1 for the other species. Small antelopes, i.e. steenbok (*Raphicerus campestris*) and duiker, were the most abundant, along with gemsbok (*Oryx gazella*), known for being the most arid-adapted large antelope [74, 75]. In contrast, blue wildebeest and springbok were notably few, reflecting their significant population declines in recent decades [63, 65, 76]. Overall, dry season densities tended to be systematically lower for all species, compared with the wet season.

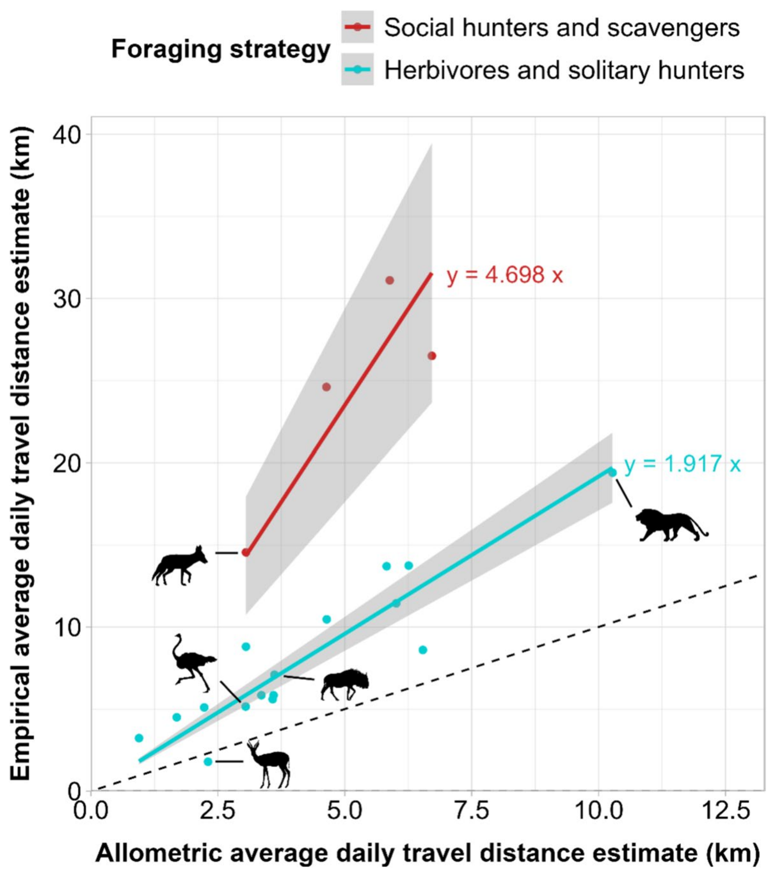

Fig. 4 Computation of empirical $\widehat{M}$ as a simple linear function of allometric $\widehat{M}$ for the two foraging strategy groups, with a 95% confidence interval (in grey). The black dashed line represents the scenario where empirical $\widehat{M}$ and allometric $\widehat{M}$ are equal ($\beta_1 = 1$). The data points for springbok, ostrich, lion, blue wildebeest 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); blue wildebeest by Graham Montgomery from PhyloPic (CC BY 4.0); ostrich, lion and black-backed jackal from Phylopic (PDM 1.0)

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 [10, 12, 13, 77, 78]. Like any technique, track surveys present some limitations and challenges [39–41]; however, they often provide the best cost–benefit approach. A promising, and still underused, method to alleviate some of these challenges is the FMP formula, i.e. an absolute animal density estimator that converts the 'number of tracks' along transects into the 'number of animals' by integrating animal detectability ($\widehat{p_1}$). The FMP formula requires an estimate of the species' average daily travel distance ($\widehat{M}$), whose accuracy is key for obtaining reliable population density estimates. Our study provides a detailed methodology for systematically trailing animals to derive accurate empirical $\widehat{M}$ that also meaningfully includes Indigenous knowledge. By adding the five species trailed in this study to existing literature data, we refined the use of allometric relationships to derive surrogate $\widehat{M}$ for Kalahari species based on their ecology. Finally, we demonstrate the potential and value of research and conservation projects designed in collaboration with local communities.

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 24 h period. Trailing is a real alternative to GPS tagging, currently widely used for data collection on animal movements [79]. Trailing offers higher control and adaptability in data collection, non-invasively and likely at a lower cost (c. 110 USD per trailing in this study). It allows for (1) collecting data on multiple independent

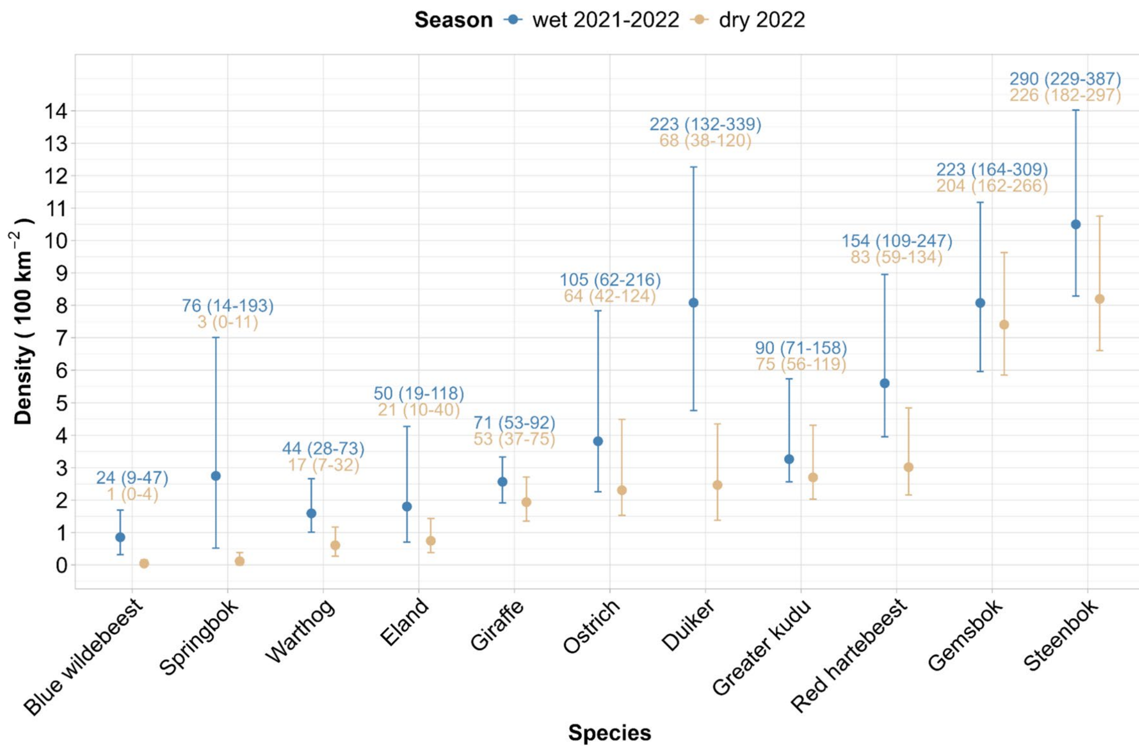

Fig. 5 Population density estimates per species per season in KGR and southern CKGR, Botswana. On top of the error bars are indicated the species abundance estimates ± bias corrected and accelerated 95% confidence intervals, calculated for the track survey study area of 2761.56 km^2

individuals or groups, only biased by those that are visible, largely preventing unrepresentative samples linked to intraspecific variability in movement behaviours [45, 80], (2) proactively spreading trailing efforts across space or time to capture natural spatio-temporal variation in species movement, (3) collecting detailed information on movement tortuosity (e.g. in [81]) while avoiding biases introduced by movement interpolation between GPS-tag fixes [82], and (4) providing an opportunity to involve and value Indigenous knowledge. Furthermore, trailing can provide more than just movement data owing to the impressive ability of Indigenous trackers to accurately interpret the target's behaviour along the trails (e.g. resting, foraging, running, fighting, digging, mating, etc.) [83]. Such data are still challenging to obtain by other means at comparable resolution, except by visually following habituated animals [49, 84], which risks occasionally altering their natural behaviour. Movement and behavioural trailing data can be correlated with various environmental variables at fine spatial and, to a lesser extent, temporal scales to reveal species' habitat use, responses to environmental variation [85–87], and interaction with anthropogenic structures (e.g. fences [88]).

Although effective for large to medium-size herbivores, our trailing method may require adaptation for different species according to their specific ecology. A slightly humid or softer soil can enhance track imprinting of soft feet/padded species (e.g. ostrich), and practitioners should avoid spotting single animals around large pans (hard soil), especially in the dry season. Smaller diel animals may have home ranges too small to forward trail them without impacting their movements. In such a case, Keeping & Pelletier [51] successfully estimated steenbok daily travel distances by spotting and back trailing individuals 24 h after rain, using raindrop-marked tracks as an endpoint —an approach suited only to abundant, visible species in the wet season. The burrows of some nocturnal species can be used as a starting point to back or forward trail their movements of the previous night, as done with aardvark [10] and porcupine (Leopard Ecology & Conservation, unpublished data). In low density environments, camera traps placed at animal activity hotspots can help spot targets on day 1, where photos reviewed for midday sightings substitute live spotting. For particularly rare or elusive species, GPS tagging using high frequency fixes might still be the most effective method for collecting daily travel distances —provided distances between fixes are reliably estimated, such as through continuous-time movement models (ctmms) (https://ctmm-initiative.github.io/ctmm/). GPS tagging can also be used to guide back trailing of potentially dangerous animals.

Regardless of the technique used to acquire movement data, the reliability of $\widehat{M}$ depends on how well it represents the true movement length of (1) the species, (2) where and (3) when the track survey is conducted. The best strategy —collecting empirical $\widehat{M}$ for every track survey and species— is often impractical. Therefore, surrogate $\widehat{M}$ are often necessary. First, when no empirical $\widehat{M}$ is available for a surveyed species, a reliable surrogate can be computed allometrically, calibrated to the region and the species ecology. We found 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. Indeed, brown hyenas (*Hyaena brunnea*) and black-backed jackals primarily scavenge and opportunistically hunt small, sparsely distributed food items, leading to extensive travel to meet daily subsistence needs in the Kalahari [49, 89, 90]. African wild dogs (*Lycaon pictus*) routinely commute in packs, flushing out prey, then engaging in multiple opportunistic cursorial chases [71]. Such a hunting strategy likely drives their wide-ranging behaviour, along with the need to avoid apex predators [91]. In contrast, felids travel less, relying on stalking or ambushing their prey rather than scavenging [92], which explains why, like herbivores, their $\widehat{M}$ scales more slowly with body size. Second, when empirical movement data exist for the surveyed species, spatial surrogates for $\widehat{M}$ should come from nearby areas with similar environmental conditions that drive comparable movement patterns to those of the track survey region. Otherwise, $\widehat{M}$ may be highly inaccurate —for example, spotted hyenas (*Crocuta crocuta*) in the Masai Mara travel about half the daily distance (12.4 km [93]) of those in the Kalahari (26.5 km [49]). Such $\widehat{M}$ can be sourced from growing open-source databases (e.g. Table 1 and [13] for the Kalahari; Movebank worldwide). Third, temporal surrogates for $\widehat{M}$ should also come for a period when species movements are comparable to those of the track survey period, an element that likely varies among species and regions. In the five species we trailed, no major temporal trend in $\widehat{M}$ was observed within the cold dry season, besides the natural day-to-day variability expected in movement behaviour. Therefore, $\widehat{M}$ can be appropriately estimated by averaging a sufficiently large sample of movements collected over that time period. This aligns with our expectations, as environmental variation in the Kalahari is primarily seasonal [23]. Consequently, the influence of seasonality on $\widehat{M}$ warrants further investigation. For instance, food and moisture availability decreases in the dry season, potentially forcing animals to move further daily to meet their resource needs [94, 95], e.g. + 13% for giraffe (*Giraffa giraffa*) [96]. Cooler dry season months (May to August) may also favour midday movements, unlike hotter periods [97, 98], e.g. + 11% for blue wildebeest [99].

Depending on how good surrogate $\widehat{M}$ are expected to be (i.e. the magnitude of species, spatial or temporal variation), practitioners must weigh whether obtaining specific $\widehat{M}$ is worth the gain in density estimate accuracy. For monitoring purposes, a good surrogate does indeed not need to be perfectly equal to the true species' average daily travel distance, just to differ from it substantially less than the variation in animal density sought to be detected [100]. In our case study, we applied the same $\widehat{M}$ across seasons for each species and still found consistently lower abundance in the dry season. This aligns with prior studies [101, 102] showing that Kalahari populations typically decline during the dry season, as mortality increases due to food and water scarcity and is no longer offset by births. Some species, such as blue wildebeest, may also seasonally move to areas providing better conditions during the dry season [103, 104]. If dry season $\widehat{M}$ exceeds wet season $\widehat{M}$, the observed seasonal difference in abundance would be even more marked. The opposite is also possible, although unlikely to the point of inversing seasonal trends in abundance. For instance, duiker likely have a higher $\widehat{M}$ in the wet season than in the dry, as density estimates differ unexpectedly by a factor of three between seasons (Fig. 5). While our results suggest that seasonal differences in $\widehat{M}$ are likely limited for most species, they should not be dismissed immediately, especially when seasonal movement or migratory patterns are present [99, 105, 106].

Finally, our case study on monitoring wildlife density ($\widehat{D}$) via the FMP highlights that not only $\widehat{M}$ is important: adequate track survey design and sampling effort are too [23, 51]. In our results, this is reflected in some discrepancies with local knowledge: springboks, present as at least 3–4 herds, were estimated at only 3 individuals in the dry season. This suggests that local variations in density were not surveyed in proportion, as transects skirted rather than crossed pans, i.e. springboks' primary habitats [73]. Eland densities may also be underestimated, as large herds are occasionally seen north and northwest of the study area, where transect coverage is limited. Then, large uncertainty around $\widehat{D}$, as visible in Fig. 5 for some species, can arise from both variability in $\widehat{\frac{x}{S}}$ across transects and uncertainty around $\widehat{M}$. High variability in $\widehat{\frac{x}{S}}$ often occurs in species with tortuous movements (e.g. duiker), highly variable group size (e.g. ostrich in the wet season), or when transects sample areas with marked differences in local species density (e.g. springbok). Adjusting transect design or applying post-stratification may help mitigate this variability, which is key for reliably detecting population trends over time. However, it is beyond the scope of this study.

Conclusions

Trailing and track surveys are not new methods, the interpretation of animal tracks and signs being one of the oldest human practices [107]. Alongside visually following habituated animals, these methods were common tools in wildlife studies worldwide during the last century [22, 87, 108–110]. More recently, however, they have been increasingly replaced by new technologies, which reduce field time while collecting large amounts of data simultaneously at landscape scale [79, 111]. 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 sacrifice population-level insights for detailed measures on a few individuals [45]. Rather than being exclusive, both approaches are increasingly recognised as complementary. Traditional knowledge can also help interpret and validate findings from modern approaches.

In Botswana's Kalahari, c. 170,000 km^2 of conservation landscape (including KGR and CKGR) have been increasingly surveyed using the FMP formula since 2008, offering a cost-effective alternative to aerial counts. The resulting data have recently enabled regional analyses of wildlife habitat suitability [56], connectivity [57], and natural resource mapping [112], guiding future land use planning [58, 112]. The FMP approach has also been recently applied in northern Botswana (unpublished data), Namibia [13], and other continents [16, 28] for wildlife monitoring and population management, highlighting its conservation potential and the need of ongoing improvement.

Socially, track-based approaches also resonate with growing calls to merge Indigenous knowledge with modern methods in conservation science [19, 113, 114]. Beyond their scientific contribution, such methods can involve local community members in collaborative projects to create mutual value —by reinforcing cultural identity and empowerment over resource management, formally recognising their knowledge, and providing employment opportunities and new experiences [21, 29, 113]. In particular, track-based approaches can be applied in various ecosystems were suitable substrate (e.g. snow, dust, sand, mud) and tracking skills exists [28, 115, 116]. We believe that a wider use of such participatory approaches can improve attitudes towards wildlife, promote coexistence and enhance conservation outcomes—especially where local inhabitants bear high costs of living alongside wildlife. 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.

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 survey 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 involving the detection, geolocation, species identification and count of animal tracks (i.e. footprints) that intersect transects of defined length within the study area.

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
$\widehat{D}$	Population density estimate
FMP	Formozov–Malyshev–Pereleshin
GPS	Global Positioning System
KGR	Khutse Game Reserve
$\widehat{M}$	Average daily travel distance estimate
$\widehat{p_1}$	Probability that an animal movement path intersects the total transect length at least once
$\widehat{p_2}$	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

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40462-025-00582-1.

Additional file 1.
Additional file 2.
Additional file 3.
Additional file 4.
Additional file 5.

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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 no competing interests.

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