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Monitoring wildlife abundance through track surveys: A capture-mark-recapture inspired approach to assess track detection by certified trackers in the Kalahari, Botswana

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ABSTRACT

The surveying of animal tracks is a cost-effective wildlife monitoring technique in conservation, provided the substrate is suitable for tracks to imprint and observers are skilled enough to detect and identify them. However, as with every method quantifying population abundance, it can be biased if track detectability is not accounted for. Track detectability has two components: probability $\widehat{p_1}$ for an animal movement path to intersect with the sampling unit at least once and probability $\widehat{p_2}$ of track detection. Here, we measured $\widehat{p_2}$, often overlooked, and tested to what extent it is affected by observers and sampling conditions, by applying a capture-mark-recapture approach to a driven track survey of 12 wildlife species in the Kalahari, Botswana. We also characterized and quantified disagreements between pairs of observers on the identification and ageing of tracks. Except for fresh ($\leq$24 old) tracks being slightly more detectable ($\widehat{p_2}$= 0.77 vs 0.61) and reliably identified (probability of agreement in species identification = 0.92 vs 0.87) than older tracks, we demonstrated that $\widehat{p_2}$ is high and most importantly largely constant across sampling conditions and highly skilled observer pairs. Species identification mismatches between observer pairs were rare (8% for fresh tracks) and limited to specific couples of close species, materializing into confusion rather than directional bias. Where $\widehat{p_1}$ can be accounted for in the derivation of population abundance from track counts (e.g. Formozov–Malyshev–Pereleshin formula), our results relative to $\widehat{p_2}$ validate the use of track surveys for wildlife monitoring in the Kalahari. Our conclusion is potentially applicable to a large range of environments across the globe, especially where observer skills are present among local communities, and conservation can benefit both wildlife and people, fostering their coexistence.

1. Introduction

If Earth is a treasure, Africa is surely one of its most beautiful gems, well-known for the diversity of its ecosystems stretching from

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deserts to rainforests or even ice-capped mountains. Today, it is home to a quarter of the World's biodiversity and supports the Earth's largest intact communities of large mammals (UNEP-WCMC, 2016). While there have been some success stories in African biodiversity conservation, there are also considerable challenges as a result of the difficulty in reconciling human well-being and economic prosperity with environmental conservation, particularly in the context of rapid population growth, urbanization and agricultural

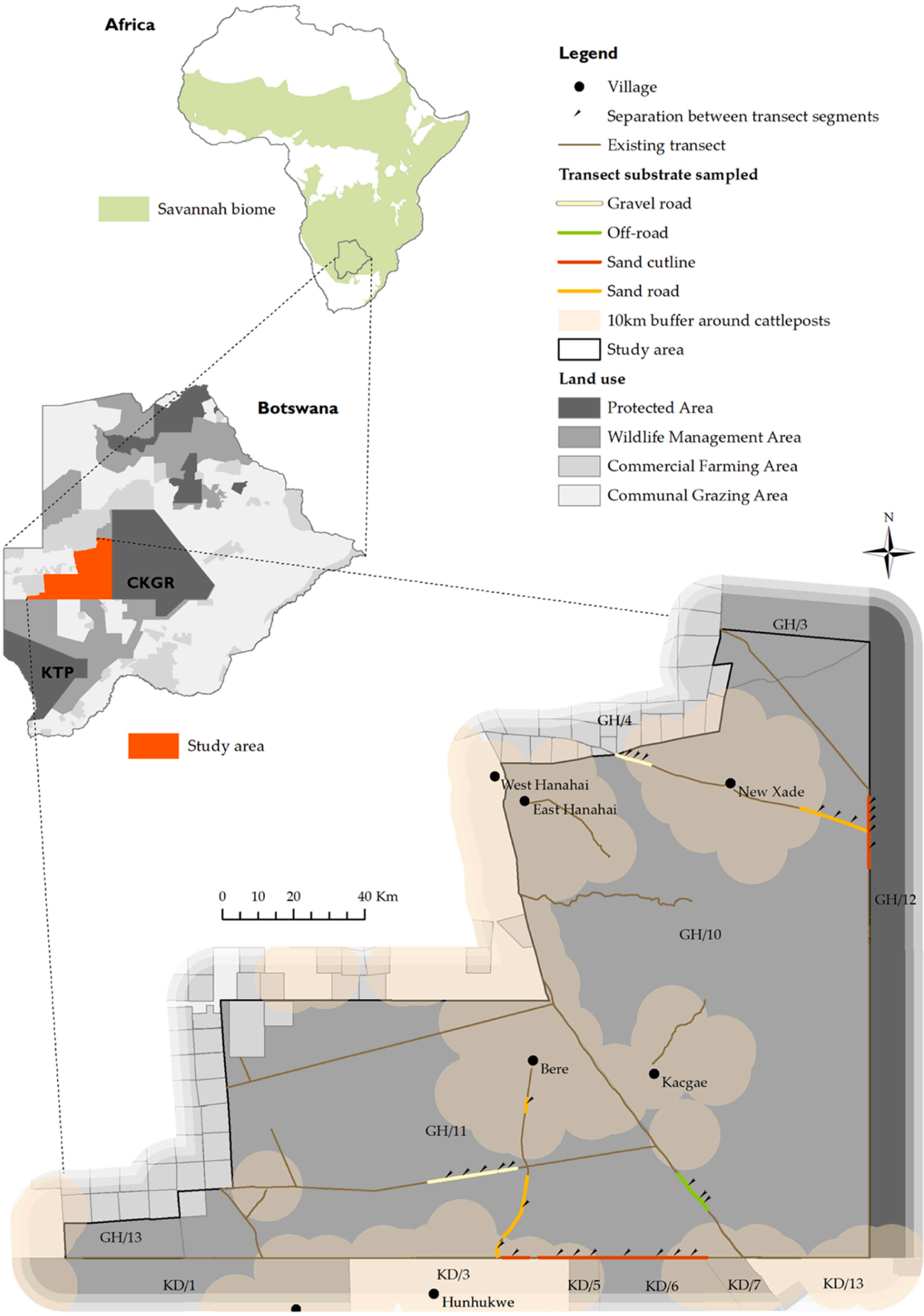

Fig. 1. The study area is situated in the Kalahari, a semiarid savannah covering a large part of Botswana. It covers four Wildlife Management Area (WMA) situated in between two major protected areas (CKGR and KTP). The transects sampled for this study are a subset of a longer set of transects crisscrossing the study area; they were chosen in order to cover the main soil substrate types found in the study area. Areas of potential high livestock track densities are indicated (i.e. 10 km buffer around cattleposts). Each transect was subdivided in segments for which the two tracker pairs alternatively switched between vehicles to allow testing for the effect of the tracker pair on the probability of track detection. Map of African savannah biome adapted from Shorrocks and Bates (2014).

development, multidimensional poverty and sometimes political and economic instability (Bauer et al., 2021; Darkoh, 2009; Kinzig and McShane, 2015; Lindsey et al., 2020). Additionally, the cost of conservation often falls disproportionately on local communities that live in or around wildlife-rich areas and were historically or currently dependent on natural resources. These costs can include exclusion from exploiting such resources, human–wildlife conflict, or sometimes loss of land; in comparison, derived benefits from conservation are often little (Allendorf, 2022; Barrow and Fabricius, 2002; Lindsey et al., 2020).

The savannah biome covers approximately 50% of Africa's terrestrial lands (Continent map in Fig. 1) and hosts numerous endemic species of both plants and animals. Together with an extremely rich biodiversity overall (Shorrocks and Bates, 2014), the African savannahs represent a significant conservation priority. Central to such a biome, in the southern part of the continent, Botswana has dedicated 40% of its lands to wildlife and its habitat since its independence in 1966 (Cooke, 1985; Parry and Campbell, 1990). Most of its wildlands are located within the Kalahari Desert (thereafter referred as the 'Kalahari'), an extensive sand-covered plain where grasses, shrubs and scattered trees create a more or less open environment depending on local climatic and soil variations (Skarpe, 1986; Weare and Yalala, 1971). The Kalahari's climate is semiarid, with annual rainfall ranging from 150 mm to 450 mm in Botswana, falling almost exclusively during the wet season (November to April) (DHV, 1980). Within the Kalahari lies the two largest protected areas of the country, i.e. the Central Kalahari Game Reserve (CKGR) and the Kgalagadi Transfrontier Park (KTP). These are interconnected by a succession of unprotected but sparsely populated Wildlife Management Areas (WMAs), and are still unfenced, enabling free-ranging wildlife to move between needed scattered resources (Country map in Fig. 1) (CI, 2010; Perkins, 2019). Botswana's commendable effort towards wildlife conservation has, however, been facing various obstacles, which have accumulated through the decades, including: the erection of veterinary cordon fences disturbing wildlife movements (Campbell, 1981; Williamson and Williamson, 1984); the expansion of cattle farming and human settlements causing human-wildlife conflict (Gross et al., 2021; Klein, 2013), wildlife habitat loss and land degradation (Abel and Blaikie, 1989; Cooke, 1985; Parris and Child, 1973); excessive hunting (illegal or not) (Campbell, 1997; Rogan et al., 2015); and the additional pressure from climate change (Kapuka and Hlásny, 2021; Nash, 2017). The main threats to the viability of the Kalahari's wildlife populations are currently the continuous growth of the cattle industry in and around WMAs (Cooke, 1985; Keeping et al., 2022b) coupled with elusive bush meat hunting (Senyatso, 2011; Thouless, 1998), and a lack of alternative nature-based livelihoods for local communities (Karunya Consulting, 2020).

Guiding and monitoring the efficiency of conservation efforts needs robust scientific background information, of which one key element is estimating wildlife abundance, its spatial and temporal variation. A large variety of field techniques nowadays exist to quantify species abundance, each with its pros and cons and often most adapted to specific groups of species. For large wildlife, the most important methods are aerial surveys (Norton-Griffiths, 1978), ground line transects (Buckland et al., 1993), satellite telemetry (Kays et al., 2015), camera trapping (Sollmann, 2018; Trolliet et al., 2014), or track and sign surveys (Keeping, 2014; Pellikka et al., 2005; Winterbach et al., 2016). Track surveys are defined here as the geolocation and identification of animal footprints across sampling units. They provide several key advantages over other methods in regions with suitable substrate for tracks to imprint such as the Kalahari sand: they can easily be applied simultaneously to multiple terrestrial species, even elusive or low-density species such as large carnivores, and on a large study area, return higher encounter rates per sampling effort, and present a lower cost (Keeping et al., 2018; Romani et al., 2018; Seidlitz et al., 2021; Silveira et al., 2003). Their main limitation resides in the need of observers with highly specialized tracking skills. In this regard, the Kalahari hosts a number of Indigenous communities descended from gathering-hunting Khoisan groups (Hitchcock, 2002; Tanaka, 1974). Their lifestyle has naturally instilled a basic level of track awareness among their members. However, in the Kalahari but also other regions around, only some individuals regularly practicing track-related activities (e.g. subsistence hunting, track-based employment, personal interest) have cultivated various levels of expertise, with a few having evolved into expert trackers (Elbroch et al., 2011; Lawrence, 2020; Liebenberg, 1990b; Stander et al., 1997). Their extensive traditional ecological knowledge is now being integrated to community conservation projects in partnership with local NGO's.

As raw counts in wildlife surveys are by nature incomplete counts of a population, the common challenge faced in all field techniques is to correct or control for imperfect detectability (Anderson, 2001). "Correcting for detectability" (such as with Capture-Mark-Recapture) allows for the estimation of absolute abundance by mathematically correcting abundance with the estimated detectability. On the other hand, "controlling for detectability" (such as with standardized monitoring schemes, e.g. for butterflies in Europe: https://butterfly-monitoring.net/) produces relative abundance indices. These indices can be compared across space and time since the detectability, unknown, is assumed to be constant (hence, correction by a constant can be ignored for comparisons). Failure to correct for detectability, or reliably test if it is controlled, is a risky strategy, as the validity of using abundance estimates for comparisons between conditions (such as species, location, time, etc.) entirely depends on detectability to be corrected (Clobert, 1995) or to be sufficiently constant, i.e. presenting a variation much lower than the variation in abundance sought to be detected (Johnson, 2008). In track surveys, two processes affect the number of track interceptions detected at a given point in space and time. One is biological, referring to the characteristics of the species itself, which results in the *individual animal detectability* ($\widehat{p_1}$). This is defined as the *probability that animal movement paths intersect with the sampling unit at least once*, so that tracks are left to be recorded. The other is the sampling process, which results in the *probability of track detection* ($\widehat{p_2}$) and is defined as the *probability that tracks are detected by observers after they were left on the sampling unit*. The probability of track detection is influenced by the observer's skills in track detection and identification, as well as the sampling conditions affecting the track visibility on the transect (e.g. survey speed, nature of the substrate, alteration by disturbance factors).

The attempts to translate track counts into population abundance, while accounting for individual animal detectability, have proven challenging. The reason lies in the difficulty to correctly model the accumulation of tracks over a time period. Born long ago in the snowy regions of Russia (Formozov, 1932; Stephens et al., 2006) and recently adapted to the Kalahari (Keeping, 2014), the Formozov–Malyshev–Pereleshin (FMP) formula offers a solution: this random encounter model converts fresh track ($\leq$ 24 h old) counts along linear transects of given length to population density estimates, using the average daily distance that animals travel (Fig. 2). By accounting for the characteristics of the animal movement path relative to transects, as well as a measure of survey effort, $\widehat{p_1}$ is intrinsically accounted for within the FMP (Keeping and Pelletier, 2014; Stephens et al., 2006). On the other hand, $\widehat{p_2}$ is typically assumed to equal 1 on the basis that observers are highly skilled, returning near-perfect accuracy in identifying large mammals and reconstructing their behaviors (Stander et al., 1997). When track surveys are done on foot with plenty of time for the tracks to be examined by expert trackers, this might hold. However, when large areas need to be sampled, track surveys are commonly performed with vehicles travelling at higher speeds than on foot; assuming perfect detection would then be unrealistic, and heterogeneity in $\widehat{p_2}$ is likely to occur as soon as sampling conditions vary spatially.

In this study, we used a double sampling survey protocol, inspired by the Capture-Mark-Recapture (CMR) technique, to estimate the probability of track detection $\widehat{p_2}$ in driven track surveys for 12 large wildlife species of the Kalahari. We determined to what extent it is affected by observers and sampling conditions (i.e. transect substrate, density of livestock tracks, age of track, and species crossing behavior on transects). We also took the opportunity of this unique dataset, collected through this double sampling approach in real field conditions, to characterize and quantify disagreements between pairs of observers on the identification and ageing of tracks. By assessing the probability of track detection, as well as identifying any bias related to disagreements in species identification and track ageing, we ultimately aim to further strengthen the reliability of inferences made from track data. While we focus here on their use for population density estimation via the FMP approach, our study is also relevant to broader applications of track data such as species habitat suitability and landscape connectivity.

2. Materials and methods

2.1. Study area

Our study area encompasses four Wildlife Management Areas (WMAs) located in the Ghanzi District of Botswana, namely “GH10”, “GH11”, “GH13” and the southern part of “GH3” (Fig. 1). WMAs correspond to game rich habitats outside protected areas, and act as buffer zones to prevent human-wildlife conflict or to protect known ecological corridors, as most large mammals in the region are nomadic (Parry and Campbell, 1990; Republic of Botswana, 1986). The four WMAs in our study form the northern part of an ecological corridor between CKGR and KTP, allowing wildlife to move around livestock farming areas (CI, 2010). They cover approximately 22, 000 km^2 and enclose four villages, each extending over a 20 km radius. A total of 45 cattleposts have been developed within the total

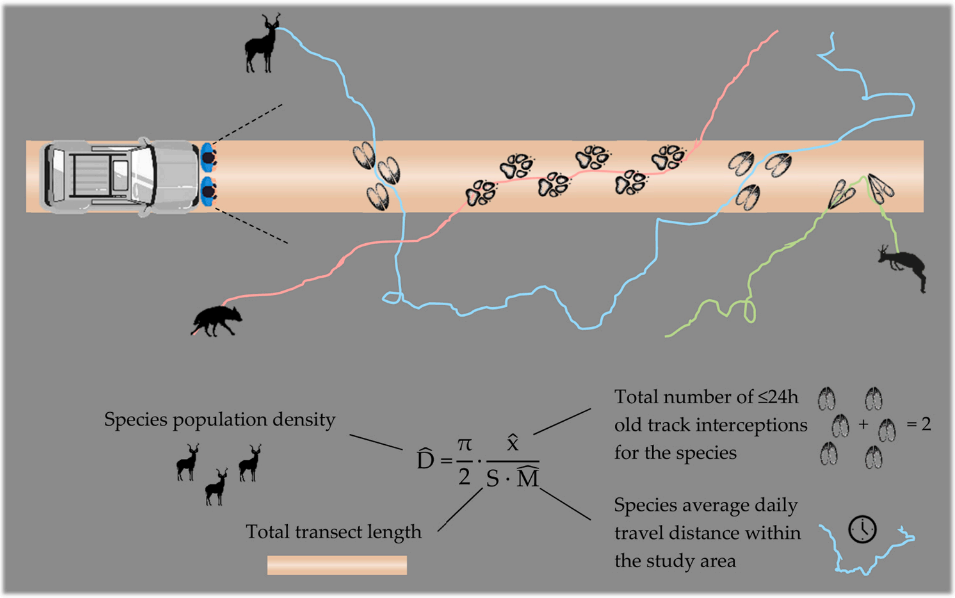

Fig. 2. Data collection in driven track surveys illustrated relative to the FMP formula approach. The space bounded by the vehicle wheels (in sand colour) is theoretically summarised as a one-dimensional transect of length S, and is related to the species movement paths of length $\widehat{M}$ in the landscape. Each of their intersections over a 24 h period appears as a series of footprints, called tracks, forming a trail on the transect. Each trail is conceptualized as one individual track interception, which are counted and summed as $\hat{x}$ fresh (≤24 h old) track interceptions along the total transect length S. The trail of individuals who walk along the transect is counted as a single track interception regardless of the number of tracks they left (e.g. brown hyena – red path). Successive track interceptions for a same species are each counted separately regardless of individuals’ identity, to abide by the random nature characterising the encounter of the animal movement path with the transect (e.g. greater kudu – blue path). Figure adapted from Keeping et al. (2018). Icon sources: https://cdn4.vectorstock.com; https://media.istockphoto.com; https://superstencil.com; https://africageographic.com; https://thumbs.dreamstime.com; Liebenberg (1990a).

area covered by the villages' radii. Here we define cattlepost as a free-ranging cattle farming system centered on an artificial water point (Perkins, 1996). An additional two cattleposts are found beyond the villages' radii, and 41 cattleposts are located within the immediate 10 km buffering the study area. Most roads are sand tracks where vehicle traffic is low, two are made of compacted gravels, and one is tarred, defining the boundary between GH10 and GH11.

2.2. Capture-mark-recapture inspired approach

In order to estimate the probability of track detection $\widehat{p_2}$, we used an approach inspired by Capture-Mark-Recapture (CMR) for a closed population (Nichols, 1992; Seber, 1986). In our case, the closed population is represented by the animal track pool imprinted along the transect at the time of the survey. In practice, each transect was surveyed twice by two data collecting teams following each other: the first team "capturing and marking" the tracks, and the second team "recapturing" them. Occasionally, the wheels of the first vehicle may obscure some individual footprints of an animal trail crossing the transect, however it is very unlikely that this would erase the entire trail. The track pool can thus reasonably be considered as identical between the two surveys. Furthermore, we ensured enough space between the two vehicles to minimize the transmission of direct visual cues from the first team to the second team, especially when the former stopped or stepped off the vehicle for a more thorough examination of the track. Nevertheless, these actions may still leave evidences on the ground, to varying degrees, potentially detectable by the second team.

2.3. Factors tested for their impact on the probability of track detection

We modelled our response variable, i.e. the probability of track detection $\widehat{p_2}$ along the total transect length, as a function of five independent factors. Further described in Table 1, these are: the tracker pair (see Section 2.4. for the composition of the data collecting team), type of substrate found on the transect, livestock track density on the transect as a wildlife track disturbance factor, crossing vs following behavior of the species relatively to the transect, and age of the track.

Where possible, we designed our survey to provide a balanced survey effort (i.e. transect length) across our five factors (Fig. 1). The latter two factors (i.e. animal crossing behavior and age of track) are entirely determined by the behavior of the wildlife, and thus we could not plan to survey them in a balanced manner. However, to achieve a balanced survey effort for the factors that could be manipulated, we ensured that: (1) we alternated the vehicle placement (first vs second) of the two tracker pairs for a similar transect length; (2) effort for transects on different substrates reflected the relative frequency of each substrate in the study region; and (3) low livestock track density was favored over high livestock track density. We preferred low livestock track density to avoid the risk of recording too few wildlife tracks in total if high livestock density resulted in very poor wildlife tracks, while still allowing us to test for the effect of livestock track density on track detection. See **Appendix A** for the detail of the survey effort across factors in terms of kilometers and number of tracks.

2.4. Transects and track counts

The track survey was conducted over 7 days at the beginning of the dry season in May 2022, along 40 transect segments ranging from 2 to 10 km in length, covering a total of 175 km (Fig. 1). Transects were chosen to sample at best the range of sampling conditions encountered across the study area as detailed above.

Table 1
Description of the factors and their different category levels tested for their possible impact on the probability of track detection.

Factor	Level	Description
tracker pair	NG pair	Lead by a Master tracker, assisted by a Tracker III (Liebenberg et al., 2018). The anticipated proficiency level for the NG pair aligns with that of a Master tracker.
	XZ pair	Lead by a Tracker III, assisted by a tracker with a Track & Sign I and Trailing III certifications (Liebenberg et al., 2018). The anticipated proficiency level for the XZ pair aligns with that of a Tracker III.
substrate	Sand cutline	Enlarged road of clear sand. Good visibility on the transect itself and for a couple of meters on either side, as deprived of vegetation.
	Sand road	Narrow road of clear sand. Good visibility on the transect only, not on its sides.
	Gravel road	Enlarged road of compacted gravel covered by a thin layer of clear finely-grained mix of sand and dust. Intermediate visibility because of more erodible sand/dust layer coupled with slightly more vehicle traffic, disturbing track trails.
	Off-road	Off-road transects on vegetated sand. Poor visibility due to vegetation and tracks not always imprinting fully on the substrate.
livestock track density	Low	The transect segment falls beyond 10 km from a cattlepost, or within 10 km but without the need of reducing speed as the wildlife track visibility is still good.
	High	The transect segment falls within 10 km from a cattlepost and the survey speed needs to be reduced due to poor wildlife track visibility inflicted by transect trampling by livestock tracks.
crossing behavior	Followers	Tracks of the 6 large carnivores and ostrich, which have the tendency of walking along the transect roads as an easier way of moving than crossing the vegetation.
	Crossers	Tracks of the 5 large antelopes, which have the tendency to cross the transect roads more and less perpendicularly without walking along.
age of track	Fresh	Tracks aged less than or equal to 24 h old.
	Older	Tracks aged older than 24 h.

Survey days started 7:30 am until 12 am, then resumed at 2 pm until 5:30 pm. We avoided the hours where sun is at its zenith to ensure the shadows in the tracks' depression are sufficient to make tracks contrasting enough with the lighter sand around it, optimizing track visibility (Fitzhugh and Gorenzel, 1985; Liebenberg, 1990b). Each of the two data collection teams consisted of a single vehicle driven by a recorder, and a pair of Indigenous certified trackers as observers. The latter sat on seats fitted on the bull bar in front of the bonnet. Driving speed was capped at 10 km h^{-1}, although this was reduced when visibility decreased. Trackers instructed the vehicle to stop to confirm track detection and identification when they judged it necessary. Once the vehicle stopped, they would only step out if they estimated a closer examination of the track was necessary for a confident identification and ageing. Upon detecting a track, the following was recorded on a specific smartphone application (Cybertracker: https://cybertracker.org/): GPS geolocation, species identity, number of individuals, and age of the tracks from 24 h to over 1 month old. The 12 species recorded were eland (*Taurotragus oryx*), gemsbok (*Oryx gazella*), red hartebeest (*Alcephalus buselaphus caama*), greater kudu (*Tragelaphus strepsiceros*), blue wildebeest (*Connochaetes taurinus*), ostrich (*Struthio camelus*), African wild dog (*Lycaon pictus*), brown hyaena (*Hyaena brunnea*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), lion (*Panthera leo*), and spotted hyaena (*Crocuta crocuta*). As per the FMP model assumptions, all footprints belonging to one single transect crossing by the same animal trail were recorded as one single track interception; different intersections of a same species with the transects were all recorded regardless of the fact they belong to the same individual (Fig. 2) (Keeping and Pelletier, 2014). The identification in terms of species and track age was not confirmed by an independent assessor or method. We only meant to identify and quantify disagreements between tracker pairs in a real-life setup, where the truth is by definition unknown.

2.5. Data analysis

Data collected in the double sampling approach were equivalent to two capture sessions as per the CMR approach, collected respectively by the first team then the second team. Capture histories for closed populations can be modeled in terms of capture probabilities, which here translate into the probability of track detection $\widehat{p_2}$ as follows:

$$\widehat{p_{2A}} = m2/n2 \tag{1a}$$

$$\widehat{p_{2B}} = m2/n1 \tag{1b}$$

Where $\widehat{p_{2A}}$ and $\widehat{p_{2B}}$ denote the detection probability of an existing track for the first and second sampling session respectively, i.e. here collecting Team A in the first vehicle and B in the second vehicle; *n1* is the total number of tracks collected by Team A; *n2* is the total number of tracks collected by Team B; and *m2* is the number of tracks collected both by Team A and Team B (See **Appendix B** for the details of the approach). Counting *m2* required to identify the tracks "recaptured" by Team B among those "marked" by Team A. Contrary to many CMR applications, tracks could not be physically marked here to avoid they would automatically be detected by Team B. We therefore used a track matching procedure based on specific criteria in terms of distance between the track location, similarity in terms of species identification and of track age estimation (See **Appendix C** for the details of the track matching procedure).

Finally, once each track collected by each team was labelled either as a double detection (by Teams A and B) or a single detection (by either Team A or B) event, we proceeded to a four-step statistical analysis:

(1) *Probability of track detection*: First, we estimated the overall probability of track detection and the total number of existing tracks following the two-step CMR approach.
(2) *Variables affecting the probability of track detection:* Second, we analyzed all recorded tracks to determine which factors affect the probability that a track was detected by both teams. We used a logistic model (SAS, PROC LOGISTIC) on the probability of double detection (Y=1) versus the probability of detection by a single team (Y=0), according to the following variables: tracker pair in Team A (i.e. first vehicle), substrate, age of track, crossing behavior (and all their 2-way interactions), and livestock track density.
(3) *Difference between the two tracker pairs:* Third, we analyzed the tracks recorded by one tracker pair only to determine the factors influencing which pair recorded the track and which pair missed it. We fitted a logistic model on the probability that a track was detected only by NG pair (Y=1) versus only by XZ pair (Y=0), according to the following factors: substrate, age of track, crossing behavior (and all their 2-way interactions), and livestock track density.
(4) *Track identification*: In a fourth step, we analyzed the agreement in species and track age descriptors of tracks detected by both tracker pairs. We tested for the impact of sampling factors via two logistic models: the probability of a species identification disagreement (Y=1) versus agreement (Y=0) according to age of track, crossing behavior, substrate; and the probability of track age disagreement (Y=1) versus agreement (Y=0) according to substrate and crossing behavior.

3. Results

In total, 1612 tracks were recorded (*n1* = 1251 by Team A and *n2* = 1127 by Team B), among which *m2* = 766 detected by both teams.

3.1. Probability of track detection

The probability or track detection $\widehat{p_2}$ can be estimated at 0.68 (766/1127) for Team A (first vehicle) and 0.61 (766/1251) for Team B (second vehicle). For fresh tracks (≤24 h old) more specifically, it goes up to 0.77 and 0.75 respectively. The total number of existing tracks can then be estimated at 1841 (1251/0.68): 766 recorded by both teams, 485 by Team A only, 361 by Team B only, and then 229 tracks that were missed by the two teams.

The very slight difference in $\widehat{p_2}$ between data collecting teams confirms that the erasing effect created by the first vehicle wheels is very small in reality. Conversely, a strong registration effect of Team B detecting evidences of Team A stopping or stepping off the vehicle would have yield nearly identical $\widehat{p_2}$, which is not the case. We do however observe a marginally significant higher probability of double track detection when the NG tracker pair was in the first vehicle (0.52 vs 0.44, $X^2 = 3.25$, df = 1, pval = 0.071). This may indicate a slight information transfer from the most experienced NG tracker pair in the first vehicle to the XZ pair in the second vehicle; so, if a registration effect exists, it is quite small. It is also worth noting that standard track surveys are, contrary to this study, typically done with a single vehicle per transect and in areas with very low traffic, making these erasing (at least for fresh tracks) or registration effects absent.

3.2. Factors affecting the probability of track detection

The probability that a track was detected by both teams was mainly affected by its age, with a different impact for crossers and followers (See **Appendix D** for full model output tables of all statistical analyses): fresh tracks (≤24 h old) have a higher probability of being detected (0.77; $X^2 = 31.28$, df = 1, p value < 0.0001) with no difference between crossing behaviors, while older tracks (>24 h old) are less detectable (0.61; $X^2 = 31.28$, df = 1, p value < 0.0001), especially for followers (crossers: 0.67 vs followers: 0.55; $X^2 = 5.18$, df = 1, p value = 0.023) (Fig. 3). This corroborates the fact that fresh tracks have more defined contours, are less disturbed by eroding factors, and are less covered by organic materials making them more visible on the transect than old tracks. Crossers are large antelopes that are more likely to cross as a larger group relative to followers, which are mostly large carnivores and thus more solitary. Therefore, old antelope tracks might be more detectable than those from large carnivores when they are part of a larger track set, which is more obvious to the eye than a single animal trail.

Finally, we found a slightly higher probability of track detection on sandy substrates compared with the two others (0.73 vs 0.65; $X^2 = 3.59$, df = 1, p value = 0.058). This corroborates with our hypothesis about higher track visibility on clear sand relatively to gravel road and off-road transects. On off-road transects, the discontinuous grass cover on the sandy substrate limits visibility of tracks to a small portion just in front of the trackers. On gravel roads, the sand/dust layer covering the transect is thinner than on sand roads and cutlines, causing the tracks to have less relief on a substrate. The sand/dust color is also whiter and therefore more prone to cause glare closer to midday. Gravel roads also have typically more traffic, causing animal tracks to be more quickly erased and fragmented, impeding detection. Slow driving speed (≤10 km h^{-1}) most probably compensates largely for difference in track visibility between substrates.

3.3. Difference between the two tracker pairs

The comparison of tracks detected solely by one tracker pair versus the other one indicated that the most experienced pair (i.e. NG pair) had a higher probability of track detection in more difficult conditions only: mainly for fresh or crossers' tracks off-road, and older tracks on gravel road ($X^2 = 17.94$ and 12.99, df = 3, p value = 0.0005 and 0.005 for the substrate * age of track and substrate * crossing behavior interactions respectively) (Fig. 4**A & B**). As explained in the previous section, off-road and gravel road transects offer conditions that are less optimal in terms of track visibility. Old tracks on gravel road transects are particularly difficult to see as their fine sand/dust is more erodible relatively to the coarsely grained sand characterizing the other substrates.

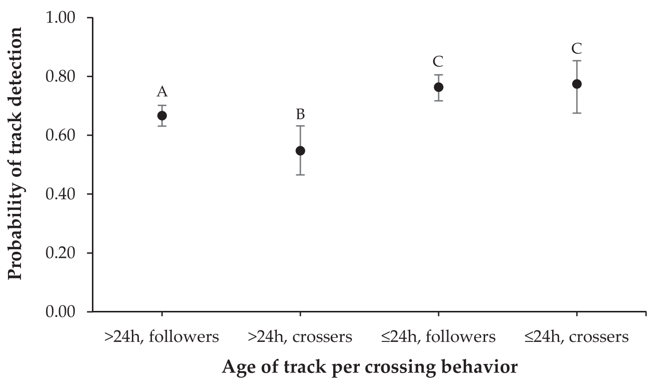

Fig. 3. Probability (estimate ± 95% CI) of track detection (double detection, i.e. by both Teams) according to the age of track and the wildlife crossing behavior. Means with the same letter are not significantly different (Student posthoc group comparisons at the 5% alpha level).

3.4. Track identification and ageing

In terms of species identification, the two tracker pairs agreed on 81% of the 766 tracks detected by both teams, increasing to 92% when considering fresh tracks only. This agreement was lower for crossers (0.77, 486/628) than for followers (0.95, 131/138). For followers, species disagreement was limited to specific couples only: 4 leopard - cheetah, 1 lion - leopard and 2 spotted hyena - brown hyena. For crossers, the higher species disagreement was mainly due to the frequent confusion (0.29, 119/412) between two species known to leave very similar tracks, gemsbok and red hartebeest, being also among the most abundant large species in the area. Overall, the logistic model analysis confirmed this: the probability that the two tracker pairs disagreed on the species identification was lower for fresh than for older tracks (0.08 vs 0.13; $X^2 = 7.04$, df = 1, p value = 0.008) and for followers' than for crossers' tracks (0.05 vs 0.20; $X^2 = 15.98$, df = 1, p value <.0001). Again, species identification is expectedly more reliable for fresh tracks due to their better state of preservation.

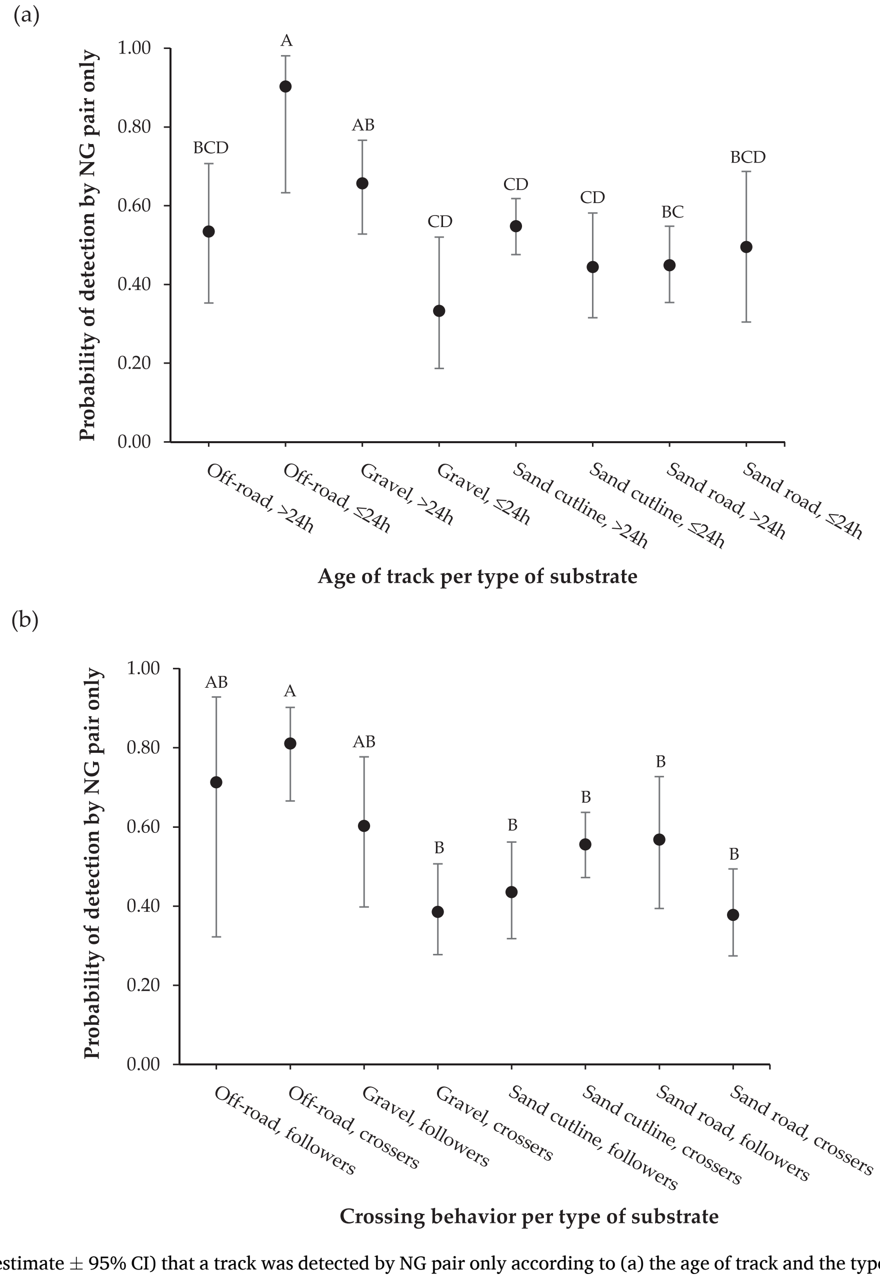

Fig. 4. Probability (estimate ± 95% CI) that a track was detected by NG pair only according to (a) the age of track and the type of transect substrate, and (b) wildlife crossing behavior and the type of transect substrate. A probability of 0.5 means that the two tracker pairs were equally likely to detect or miss a track; a probability of >0.5 means NG pair had a better probability of track detection than XZ pair, and the opposite is true when the probability is <0.5. Means with the same letter are not significantly different (Student posthoc group comparisons at the 5% alpha level).

In terms of track ageing (fresh versus older), the two tracker pairs agreed on 88% of the tracks (672/766), with no difference between crossing behavior (0.86=118/138, for followers; 0.88=554/628 for crossers). The probability that the two tracker pairs disagreed on the age of track depended only on the substrate, with a higher value of disagreement probability (0.23; $X^2 = 11.53$, df = 3, p value = 0.009) on gravel compared with other substrates. This is probably due to the fine sand/dust of gravel roads that is more erodible than the coarsely grained sand of the other substrates: the age interpretation becomes more quickly challenging.

Importantly, the disagreement in either species identification or track ageing did not result in an important difference in the total number of tracks that were recorded by each tracker pair over the total transect length. This suggests that both pairs were prone to some specific confusions (confounding Y↔Z) with no directional bias (confounding mainly Y→Z or mainly Z→Y), leading to errors that, for the most part, cancel each other in terms of final track abundance. Regarding track ageing, this confusion is consistently observed at species level as well, where the sample size is sufficient. As for species identification, one tracker pair, however, exhibited a much higher proportional count for spotted hyena and blue wildebeest; it might suggest a potential directional bias, yet the very limited total track count for both species makes such a conclusion uncertain given the risk of a false positive error. Detailed species and track ageing matching results are given in **Appendix E**.

4. Discussion

Assessing the reliability of observers in detecting and correctly identifying tracks or other indirect signs has generally received little attention in wildlife surveys (Lawrence, 2020). It is even more rare that studies assess the impact of other sampling variables on their probability of detection on transects. Instead, most studies using indirect animal signs (e.g. tracks, feces) estimate track detectability as a whole, without differentiating between its components of individual animal detectability $\widehat{p_1}$ (the animal leaves a track on a sampled unit at least once) and probability of track detection $\widehat{p_2}$ (the track is detected during sampling). Possible sources of heterogeneity in the latter (sampling process) are also overlooked or only partially accounted for (Hayward et al., 2002; Karanth et al., 2011; Linnell et al., 2007; Romani et al., 2018; Thorn et al., 2011). Our study is to our knowledge the first published to apply a Capture-Mark-Recapture (CMR) inspired approach to explicitly and independently quantify the probability of track detection $\widehat{p_2}$ in real field conditions. It does so by exploiting the knowledge that the real, but unknown, set of tracks, can be considered identical for the two data collecting teams driving the transect immediately one after the other. The only alternative approach for quantifying $\widehat{p_2}$ would be to create a known set of tracks as the reference. However, this approach is not compatible with a real field case where thousands of animals freely move across hundreds of kilometers of transects.

The main conclusions of our study are: (1) $\widehat{p_2}$ is particularly high relatively to classical values of detectability obtained with various animal sampling methods, and is remarkably constant across observer pairs and sampling conditions; (2) there are species identification and track ageing mismatches between pairs of observers, although the former is vastly limited to specific couples of close species. Notably, they materialize into confusion (bidirectional error, e.g. confounding species Y and Z) rather than a tendency to preferentially identify one species or track age class over another (unidirectional error, e.g. confounding species Y as Z more often than Z as Y). Identification mismatches are also much more frequent when tracks are old.

4.1. Track detection in driven surveys is remarkably high and constant over a range of conditions

We estimated an overall probability of track detection of 0.68 on driven transects, increasing to 0.77 when only considering fresh tracks (≤24 h old). This is highly encouraging when we consider comparable probability of detections (conditional of the species presence) from various alternative animal abundance estimation methods. For example, a probability of <0.5 in CMR of flying adults was obtained for the butterfly, *Boloria eunomia,* in Belgium (Schtickzelle et al., 2002; Schtickzelle, Unpublished data), 0.4–0.8 in live-trapping for the mouse, *Pseudomys novaehollandiae,* in Australia (Burns et al., 2019), 0.57–0.86 in double surveys (direct sightings) of several river bird species in USA (Fletcher and Hutto, 2006), 0.05–0.54 in underwater visual census of reef-fish in Tanzania (MacNeil et al., 2008). These probabilities can also decrease with the animal distance from the camera for several terrestrial mammals such as in camera trap surveys in Côte d'Ivoire (Cappelle et al., 2021). This confirms the efficiency of the survey protocol we used, in particular the choice of (1) a limited driving speed; (2) a survey period where major climatic disturbances are rare; and (3) areas where vehicle traffic, susceptible to erase tracks, is light. First, the survey driving speed was capped to a maximum of 10 km h^{-1}, the average cruising running speed for a human, based on the experience of several years of track surveys done by researchers in the Kalahari (D. Keeping, pers. comm.). Such speed was also used by Midlane et al. (2014, 2015) in Zambia, and is more conservative than the 10–20 km h^{-1} of Funston et al. (2010) and 20 km h^{-1} of Stander (1998). Second, at the beginning of the dry season, tracks persist longer because of decreased weathering (no more rain, no strong wind yet). Third, although some transects may undergo slightly higher traffic levels, it cannot be disentangled from the substrate categories (i.e. traffic intensifies: gravel road>sand cutline/road>off-road). However, all the space not directly beneath the tires still remains undisturbed and therefore animal trails remain detectable even if some individual footprints are erased. In line with this, both Midlane et al. (2014) and (2015) and Kamjing et al. (2017) did not find any impact of the transect disturbance by other vehicles on the probability of track detection.

Even if high, $\widehat{p_2}$ was clearly lower than 1 in our driven track survey: some existing tracks are missed, even by highly skilled trackers, contrary to the FMP assumption. This highlights the importance of measuring $\widehat{p_2}$, in order to adjust the total track count along the survey length to an estimate of its true number. If not possible, it is necessary to ensure that $\widehat{p_2}$ is sufficiently constant over space and sampling conditions to be considered as "controlled". If $\widehat{p_2}$ is controlled, then observed differences in track abundance, although not indicative of absolute estimates, can still be compared to each other. In this regard, our results suggest that $\widehat{p_2}$ is relatively controlled:

other than the fact that fresh tracks were more detectable and more reliably identified than older tracks due to their better state of preservation, $\widehat{p_2}$ was not or only slightly affected by all other tested variables. With over 1000 tracks recorded by each team, statistical power in our study was large enough to be confident this is not a type II error case (existing effect is missed). First, tracks only tend to be slightly more detectable on clear sand substrates, which offer more optimal track visibility, and ageing them is slightly less reliable on gravel roads whose substrate is more erodible. Previous studies of driven surveys on sandy soils found that substrate quality in terms of track visibility did not affect the probability of track detection, possibly due to low driving speed (Funston et al., 2010; Gompper et al., 2006; Hines et al., 2010; Thorn et al., 2011). Significant impact of substrates on probability of track detection was only found when substrates were substantially different from one another (e.g. comparing mud, sand, snow, leaf litter, rock) (Jeffress et al., 2011; Schooley et al., 2012; Van Dyke et al., 1986). Second, we evidenced that the observer pair led by the most experienced tracker has slightly more chances to detect tracks, but only in the most challenging conditions, as already observed for other study systems (Jeffress et al., 2011; Schooley et al., 2012; Seidlitz et al., 2021). The difference was nonetheless very small (5%), supporting the hypothesis that variations in detection among observer pairs, if not null, are limited, provided the team leaders have a sufficiently high level of skills and experience to ensure quality control of the data collected. This is a reassuring result for large wildlife track surveys, although formal proof would require replicating our study with a larger number of tracker pairs.

While $\widehat{p_2}$ was shown to be remarkably constant in space, what about its temporal variations, between years and between seasons? We argue that $\widehat{p_2}$ is also very likely to be highly constant from year to year if sampling conditions stay the same (highly skilled observers as team leaders, type of transects, data collection protocol, survey period). More caution must be exercised if the survey period varies within the year depending on how much surveys conditions would differ, modifying track visibility. Our results are reassuring in this regard as the probability of track detection was only marginally affected by transect difference in terms of visibility (e.g. clear sand transects vs others, including vegetated off-road ones). Any decrease in transect visibility can be at least partially compensated for by reducing the survey speed. If there are still good reasons to assume a decrease in track detection probabilities in certain seasons, care must be exercised when making inference about temporal trends in track abundance. Given our results, we argue that the individual animal probability $\widehat{p_1}$ is more likely to show temporal variations, both between seasons and years, than the probability of track detection $\widehat{p_2}$. This must be considered too, for instance by estimating season-specific parameters related to $\widehat{p_1}$ (e.g. the species average daily travel distance for the FMP) to compute animal abundance from track abundance.

4.2. Species and track age confusion is limited but emphasizes the importance of observer skill level

We showed that confusion in species identification and track ageing is overall relatively uncommon, but does happen. Species mismatch between the two tracker pairs is mainly confined to specific species with very similar tracks. Misidentification between similar species is commonly reported in the literature, e.g. for *Lontra canadensis* tracks (Evans et al., 2009), medium to large carnivore tracks (Smallwood and Fitzhugh, 1995), or *Lynx lynx* tracks (Linnell et al., 2007). We also demonstrated that observer agreement in track ageing (fresh vs older tracks) is good (0.88), although imperfect. Track ageing is one of the most difficult aspects of tracking, and even the best trackers in the Kalahari display some level of imperfect accuracy while ageing tracks (Liebenberg, 1990b). Altogether, these results emphasize the importance of observer training to reach and maintain an excellent level of tracking skills. Observing regular practice has proven to improve tracking skills over time (Evans et al., 2009; LEC, Unpublished data).

It is nonetheless worth noting that disagreement in both species identification and track ageing results in confusion but not bias towards some species or track age category, at least for highly skilled observer pairs. Therefore, we can hypothesize the impact on the total track count to be minimal due to errors cancelling themselves out on average along the total transect length, as we observed here. As for track ageing, dragging the tracking surface to clear it 24 h prior to the survey will ensure an accurate count of fresh tracks only, as performed in some studies (Keeping, 2014; Silveira et al., 2003). However, it might not be worth the substantial increase in time and cost given the cancelling effect of age confusions.

4.3. Implications for track data applications

The FMP method, as some other track survey analytical frameworks (e.g. Funston et al. 2010), only uses fresh tracks for conversion of track counts into population densities. In the case of a vehicle driven survey on sandy substrate, we showed that the probability of fresh track detection $\widehat{p_2}$ is 0.77; hence, the absolute estimates of animal density will be underestimated to some extent. Since the probability of track detection has proven to be largely constant across other sampling condition variables (i.e. "controlled"), the FMP model can at least ensure the generation of reliable values of relative population density. Practitioners must then decide if additional efforts should be spent to estimate $\widehat{p_2}$, and therefore how many tracks were missed by observers, through a similar study to ours, in order to generate absolute estimates of population density by "correcting" the number of recorded tracks by $\widehat{p_2}$. This might not be worthwhile where, depending on the survey design characteristics, $\widehat{p_2}$ is likely sufficient high, generating a limited underestimation of existing number of tracks (hence abundance), especially compared with the measurement errors potentially surrounding other parameters related to $\widehat{p_1}$.

Where both components of track detectability $\widehat{p_1}$ and $\widehat{p_2}$ are measured or controlled, the track index (i.e. the number of track interceptions per sampling unit) can also be used as a proxy to assess the relationship between actual wildlife abundance and various ecological variables. This approach can help highlighting wildlife key habitats (Keeping et al., 2022a), distribution (Hines et al., 2010), and landscape connectivity (Keeping et al., 2022b). This can prove useful in many cases where track counts are too low to calculate density estimates at a spatial scale fine enough to test covariates' impact on them. Along the same lines, the inclusion of older tracks in the dataset could benefit the sample size, as well as reduce zero-inflated model issues due to too many fine scale track absences. However, the detection probability of old tracks must stay constant across sampling conditions for a given age category. Repeated sampling in time would also be appropriate to generalize inference within a relevant time frame for which $\widehat{p_1}$ is assumed constant (e.g. season), to minimize false absence of tracks.

4.4. Global perspectives and implications for community conservation

In view of our result relative to $\widehat{p_2}$ and former studies addressing parameters related to $\widehat{p_1}$ within the FMP framework in particular (Keeping and Pelletier, 2014; Stephens et al., 2006), track surveys have the potential to constitute a robust field technique to assess relative or absolute population abundance. They can be applied to virtually any terrestrial species leaving recognizable tracks, in many regions in the world offering a soft enough substrate for them to imprint and be seen.

In order to maximize $\widehat{p_2}$ in driven surveys, practitioners must ensure to survey: (1) where and when disturbances are mild; (2) in daytime periods when track visibility is good; (3) at low speed adjusted by observers; (4) with observers whose tracking skills and ecological knowledge have been assessed and maintained to an excellent level. Principles of good study design must still apply to minimize heterogeneity in $\widehat{p_2}$, by aiming for the factors possibly affecting it to be as homogeneous as possible across the sampling units and time. In walking track surveys, $\widehat{p_2}$ is likely to be close to 1, although it would be interesting to formally test this assumption. Finally, the accuracy and precision of population density estimates derived from track counts could still be improved by identifying optimal levels of survey effort relative to animal true density, adequate sampling unit design, as well as refining estimates of animal movement paths, all related to $\widehat{p_1}$ (Finerty, Gielen et al., in prep.).

A key element to the quality of the track data collected remains the skill level of the observers. In this regard, Southern Africa still hosts some of the best trackers in the world (Liebenberg, 1990b; Stander et al., 1997). However, some members of other communities around the globe possess similar skills too, e.g. in Siberia (Brandišauskas, 2016), Canada (Wong et al., 2011), Australia (Ens et al., 2015), Brazil (Dario, 2019), India (Lohe, 2014), Nepal (Shrestha and Lapeyre, 2018), Philippines (Hagen et al., 2016), to cite a few. Although one precious legacy of humankind, this knowledge is unsurprisingly eroding, as the wind of modern society blows in (Aswani et al., 2018; Liebenberg, 2021). The communities' involvement in track-based work is an ideal way to maintain tracking skills, value cultural identity and Indigenous knowledge, but also provide much needed employment. Hence, it can generate both high quality data for wildlife research and conservation projects and be inclusive of local communities (Elbroch et al., 2011; Liebenberg et al., 2017). This is one avenue to renew the focus on Community Based Natural Resource Management and Payments for Ecosystem Services for these communities to receive some benefits from wildlife conservation, but also (re)appreciate wildlife's intrinsic value: "nature for people" and "nature and people" can coexist. Standardization and quantification of tracking skills, especially for research applications, is necessary to ensure accuracy and reliability of data collected. It can be done through the training and evaluation of observers via certification programs such as the Cybertracker Conservation's Tracker Certification System (Liebenberg et al., 2018), which provides a structured way to learn and achieve certification of expertise (Lawrence, 2020). Certified skills can be valued by observers and could be formally recognized by both governmental and private sectors.

Research, field techniques and analytical frameworks continuously evolve with time, and we now have tools we did not have before. The Kalahari, but also many other regions worldwide, have suitable tracking substrates and therefore the opportunity to rapidly assess wildlife populations at a relatively low cost, bringing benefits to communities living with them. So, non-exclusively to other field techniques, let's use tracks where appropriate, keep improving their analytical framework, and acknowledge them as more than just poorly understood indices.

Ethical standards

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

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CRediT authorship contribution statement

Glam Khumo: Investigation. **Zoro Zoronxhogo:** Investigation. **Nicolas Schtickzelle:** Writing – review & editing, Supervision, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Marie-Charlotte Gielen:** Writing – original draft, Visualization, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Xiko Johannes:** Investigation. **Njoxlau Kashe:** Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. Authors of this study who are Indigenous trackers did not participate to the data analysis and did not influence its conclusions about their tracking skills.

Data Availability

Data will be made available on request.

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Supplementary material

The detailed sampling effort planning (Appendix A), a description of the two sessions Capture-Mark-Recapture approach (Appendix B), the procedure for matching tracks detected by the two teams (Appendix C), detailed statistical results of the logistic regression models (Appendix D), and detailed species identification and track ageing matching results (Appendix E) are available in the Supplementary Material.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02924.

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Glossary

Track: animal footprint on the substrate. More particularly in this manuscript, "track" represents the intersection between an individual animal movement path and the transect; although appearing as series of footprints (i.e. trail) on the latter, it is conceptualized as one individual track interception.
Track set: group of track interceptions representing the intersection between the movement paths of more than one individual animal of a same species and the transect, typically occurring when animals are travelling in groups. It is recorded as one single geolocation at the time of data collection, with the number of individuals composing the track set clearly indicated.
Trail: series of footprints of a same individual animal, forming its movement path across the landscape.
Track survey: here defined as the method collecting the geolocation and characteristics of animal track interceptions found along transects of defined length within a study area.