

Chapter 2

The methodology of track surveys

I. Field techniques for animal population sampling

Thanks to new technological advances, a large variety of field techniques are now available to survey terrestrial animals for various applications, with or without capturing them. The choice of the method to use depends on the study objectives, its spatial and temporal resolutions, the intrinsic characteristic of the species, the environmental conditions, and the available budget (McComb et al., 2018). The more specific or constraining these factors are, the smaller the range of appropriate methods is likely to be.

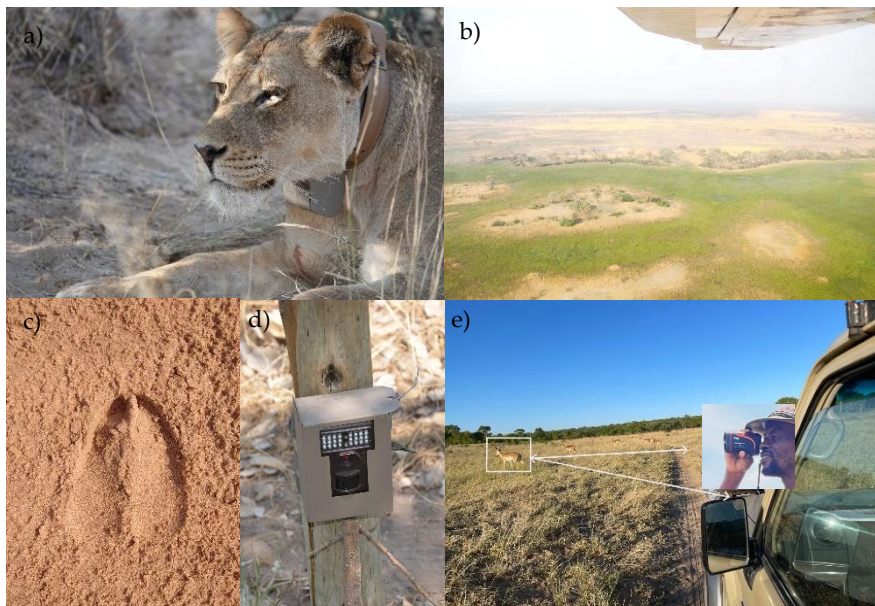


Plate 2-1 Illustration of commonly used techniques for monitoring large wildlife.

a) Satellite telemetry, b) aerial surveys, c) track surveys, d) camera trapping and e) ground line transects (distance sampling).

Photo credit: a) Leopard Ecology & Conservation, b) and c) Marie-Charlotte Gielen, d) Marie-Charlotte Gielen - Cheetah Conservation Botswana, e) Alessandro Araldi – Leopard Ecology & Conservation.

In the present thesis, studying abundance, distribution and movement of large animals of different guilds, over several years, and across large areas could a priori be undertaken with several methods: aerial surveys, ground line transects (distance sampling), satellite telemetry, camera trapping and track surveys (**Plate 2-1**).

Aerial surveys have been implemented on a regular basis by the Government of Botswana from 1987, following the methodology for transect sampling developed by Norton-Griffith (Norton-Griffiths, 1978). This technique can collect valuable data over large areas to study relative temporal changes in the abundance and distribution of large herbivore populations. However, aside from being highly expensive compared with other field techniques (Keeping, Burger, et al., 2018), this method is poorly reliable for nocturnal and less conspicuous species such as large carnivores, and even some more cryptic or solitary large herbivores. For such species, undercounting bias presents a significant challenge for accurate abundance estimation (Caughley, 1974; Jachmann, 2002).

Although more affordable, population density estimates based on ground line transects are similar to aerial survey in their vulnerability to species-specific visibility biases, due to vegetation and species-specific behaviours. Also, the accurate estimation of its detection function needs a minimum number of observations (Buckland et al., 1993), which is a requirement difficult to meet in low wildlife density regions such as the Kalahari without extensive kilometres of transects (Keeping, Burger, et al., 2018).

Satellite telemetry can be applied to more elusive species by collaring individual animals with a Global Positioning System (GPS) unit. It can return extensive numbers of highly precise spatial and temporal location data to infer animal movement and study animal behaviour, life history, space use, or habitat preference for instance (Kays et al., 2015). However, GPS telemetry studies are highly constrained by the trade-off between the sample size required for population-level inference and the high cost per GPS unit and associated expenses (Hebblewhite & Haydon, 2010; Robertson et al., 2012). Besides, collaring procedures are invasive, which implies risks for the animal. Given the multi-species aspect of this PhD study, satellite telemetry would be unaffordable, in addition to not being of use for estimating population abundance.

Camera-trapping is a very versatile method, applicable to various research questions (Sollmann, 2018; Trollet et al., 2014) including population abundance of unmarked species (Rowcliffe et al., 2008), and suitable to a large range of environments (Agha et al., 2018). Photographs typically provide high accuracy in species identification, even down to the individual level for marked species. Relatively large area extent can be sampled simultaneously, and cameras are usually easy to handle following basic training. However, depending on the cameras' placement relative to the ground and the level of sensitivity set to trigger the camera, the range of species that can optimally be

captured will be limited by their body size (Apps & McNutt, 2018). Since the species of interest in this thesis fall within a similar body size range, this is not a concern. However, when the study area is vast and remote, the initial and maintenance costs —along with risks of theft or damage by animals or people— can quickly become unsustainable. Additionally, hot climatic conditions increase the likelihood of camera failure (Apps & McNutt, 2018). Given that the study area is highly remote and spans several thousand square kilometres under the harsh conditions of the Kalahari, camera trapping may not be the most suitable method for data collection in this research.

Track surveys can be applied to multiple species simultaneously provided they leave footprints or other signs behind. They typically return higher encounter rates than aerial survey, ground line transects or camera-trapping (Keeping, Burger, et al., 2018; Seidlitz et al., 2021; Silveira et al., 2003). This is especially desirable for assessing both elusive species such as large carnivores, and low-density populations of the Kalahari. With typically lower false absence rates, the method enables the creation of more complete species distribution maps and has been shown to produce comparable population density estimates to aerial surveys and line transects with equal survey effort (Ahlsvede et al., 2019; Keeping, Burger, et al., 2018). Romani (2018) also found that the density estimate obtained through camera-trapping and track-count methods were highly correlated. Finally, track surveys are more cost effective than the above described methods, both per observation or kilometre surveyed (Keeping, Burger, et al., 2018; Romani et al., 2018; Seidlitz et al., 2021). However, track surveys need a soft substrate that allows footprints to imprint and retain their contours long enough before external factors erode them. Snow, mud, dust, and sand are particularly suitable for this purpose. Thus, the Kalahari, with its extensive sand and occasional dust cover, provides an ideal environment for studying animals through their tracks. Additionally, track surveys demand extensive knowledge of the local environment and exceptional tracking skills from the field personnel. In this regard, the Kalahari is well-suited, as it is home to expert Indigenous trackers whose remarkable skills have been passed down through generations as part of their gatherer-hunter lifestyle (Liebenberg, 1990b; Stander et al., 1997).

Although the above-mentioned methods can complement each other, track-based methods were chosen for data collection in this thesis. This decision was based on the characteristics of the species and environment studied, as well as the availability of observer expertise and its potential cultural, economic, and conservation benefits.

2. Why surveying tracks?

“Traditional techniques of field naturalists are sometimes overshadowed by newer and more technology-intensive methods. However, with slight adaptations, traditional techniques often can meet the demands of modern wildlife science.”(Beauvais & Buskirk, 1999)

When animals move through the landscape, they are more often than not leaving a sign of their presence. It can be a piece of hair or feather, disturbed vegetation, a noise, faeces, but also footprints. Many animals are in reality difficult to see directly, making such signs the first evidence of presence for many species. When the substrate is right, footprints (also called “tracks” or “spoor”, inclusive of legless animals) are the most abundant signs terrestrial animals can leave, from tiny insects to large mammals. To a point that following an animal through its tracks and secondary signs can potentially lead to it (Liebenberg, 1990b). This is precisely how our gathering-hunting ancestors survived for millennia. In fact, tracking is of much more importance than given credit for in modern days, as it might well be at the very origin of the hypothetico-deductive reasoning of scientific thinking (Liebenberg, 2021; Lombard & Gärdenfors, 2017). While interpreting animal tracks, trackers naturally engage an iterative process of confirming or refuting hypotheses based on the evidences they find around them.

Nowadays, in most parts of the world, the interest in tracks and signs has shifted from benefitting survival to a variety of applications, although still serving human curiosity and its understanding of the natural world. Animal track and sign surveys are now used frequently in animal population monitoring (Karanth et al., 2011; Kendall et al., 1992; O'Neil & Swanson, 2010; Pellikka et al., 2005; Sulkava, 2007), characterizing wildlife habitat use and impact of land use changes (Kurki et al., 1998; Lees & Peres, 2008; Moleele & Mainah, 2003; Norris et al., 2008; Soutiere, 1979; Williams et al., 2016), planning sustainable wildlife harvesting (Belova & Sezikas, 2017; Helle et al., 2016; Linnell et al., 2007), or managing invasive species (Engeman et al., 2001; Read & Eldridge, 2010).

As described above, track surveys are appealing by their relatively simple implementation while rapidly returning a large amount of data for a fraction of the costs of other methods. Notably, where substrates are suitable, they allow detection of virtually all terrestrial animals. Therefore, they may be the only practical means for studying rare and cryptic species over large areas. Tracking also involves a deep understanding of the natural world, nowadays found in some highly trained professionals or as Indigenous knowledge in

remote communities. In the latter case, track-based methods involving local community members can evolve into inclusive citizen science and participatory conservation initiatives, which can potentially be highly beneficial for both humans and non-humans. By incorporating Indigenous knowledge, they value cultural identity and promote its transmission across generations. Simultaneously, track-based work provide economic benefits to some local community members while enabling their direct involvement in wildlife research, conservation efforts or resources management. This empowerment could also help foster human coexistence with the rest of nature (Keeping, Burger, et al., 2018; Legge et al., 2024; Liebenberg et al., 2017; Lilleyman et al., 2022).

The survey of indirect animal signs may go by different names such as track or spoor surveys (e.g. sampling animal “footprints” of legged or legless animals), sign surveys (e.g. sampling animal scats or hair, involving or not genetic analysis), pellet counts for ungulates, etc. In this thesis I used the former, and refer to it as “track survey”. In the interest of clarity and consistency, I define animal track survey as the detection, geo-location, species identification and count of animal tracks across sampling units made of a soft, easily “imprintable” substrate. Another track-based method is “trailing”, which involves following (and recording relevant information as needed) an animal trail, defined as a series of footprints from the same individual animal, forming its movement path across the landscape. Track surveys are used throughout all three research chapters (Chapter 3, 4 and 5), and will be described more extensively in the following sections. Trailing is used in Chapter 4, where it will be explained in more detail.

3. The San and the art of tracking

Before diving into the methodological details of track surveys, I would like to highlight the importance of good tracking skills in this technique. The ability to consistently spot animal tracks along sampling units and identify them accurately in a short amount of time is essential to ensure the quality of the data collected and the reliability of the analyses based on them.

Indigenous inhabitants of the Kalahari, the San, are renowned for possessing such skills to a truly remarkable level. Also known as “Bushmen”, or “Basarwa” referring to the San of Botswana, they are the descendants of the oldest *Homo sapiens sapiens* grouping identified so far, the Khoisans (Chan et al., 2019), currently occupying southern African regions (Tanaka, 1974).

Historically, the San followed the nomadic gathering-hunting lifestyle of their ancestors across millennia (Liebenberg, 1990b). Although they have interacted with other socio-economic groups for at least two thousand years (Denbow & Wilmsen, 1986; Robbins et al., 2008), foraging has always been a substantial part of their activities and culture (Hitchcock, 1987). At present, while subsistence exclusively based on gathering and hunting is unlikely to exist anymore, occasional foraging still happens within San communities as a buffering strategy and as a means of diversifying their diets (Hitchcock, 2002) (Plate 2-2).

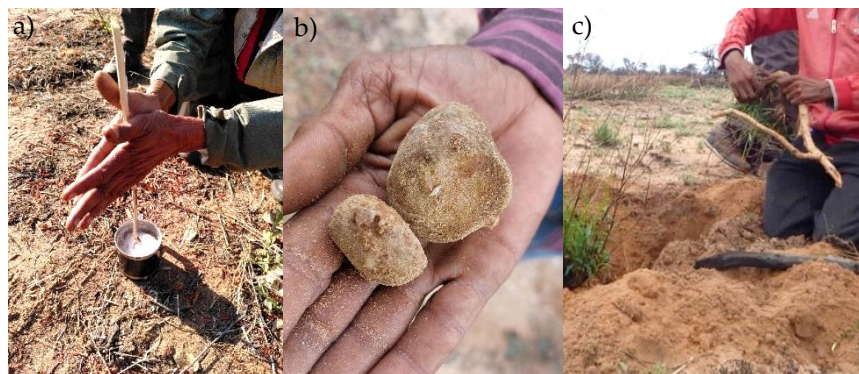


Plate 2-2 Illustration of the gathering tradition in San communities.

a) Making traditional soap from a root, a) Harvesting Mahupu – “Kalahari truffles”, b) Gathering medicinal or edible plants.

Photo credit: a) Marie-Charlotte Gielen, b) Nicolas Schtickzelle, c) Max Phale Seele – Cheetah Conservation Botswana.

Therefore, from this way of life emerged an impressive knowledge of the local fauna and surrounding environment that has been passed through generations. As Heinz (1971) points out:

“Life in such hostile surroundings as the Kalahari depends on the ability to notice what may be essential to survival. Is it, therefore, not natural that this ability of observation and deduction leads to an interest in the most important objects of a man’s environment, his own and the bodies of the animals which nourish him”

This is this over-trained propension to observation and deduction that enabled San to read the Kalahari sand like one reads a book, or more precisely to “read in between the lines” or “into the sand” as Liebenberg (1990b) clarifies. To find an animal, a tracker needs not only the technical ability to spot and identify a track (i.e., systematic tracking) but also the skill to interpret it and the signs around it (i.e., speculative tracking). The trackers need to

project themselves into the position of the animal in order to create a hypothetical explanation of what the animal was doing, when it did it, and where is it going, especially when few or poor evidence are available. A fine perception of the world, an advanced ecological knowledge, and a great imagination; an art indeed, but also a science of great value in the field of ecology and conservation.

Kalahari San communities have phenomenal trackers whose ability to interpret tracks and signs have been cultivated over a lifetime and developed to an exceptional level. The best of them cannot only identify the species a track belongs to, but also determine its sex in some species, its age group, and estimate approximately when the animal passed by. In the case of some large species, trackers can sometimes even differentiate the tracks of individual animals (Heinz, 1978; Jewell et al., 2016; Liebenberg, 1990b). Therefore, the track surveys in this thesis have been assisted by expert trackers recruited from local San communities located within my study areas. Amongst them were two of the last Master trackers still alive in the Kalahari (see **section 4.4**). The “Master” qualification is the highest recognition by the CyberTracker Conservation’s Tracker Certification System (Liebenberg et al., 2018) to Indigenous knowledge, the pursuit of new knowledge in the art of tracking, mentoring of Senior Trackers and future Master Trackers, and the development of the tracker community.

4. Track counts in practice

4.1. Study areas and sampling units

Track surveys were conducted in the northern part of the Western Kgalagadi Conservation Corridor (WKCC), covering WMAs GH3/10/11/13. Chapter 4 also includes track survey data collected by a third party in Khutse Game Reserve, located adjacent to the southern border of CKGR, and also part of the WKCC (**Figure 2-1**). The study area for each chapter will be described in detail within the corresponding section.

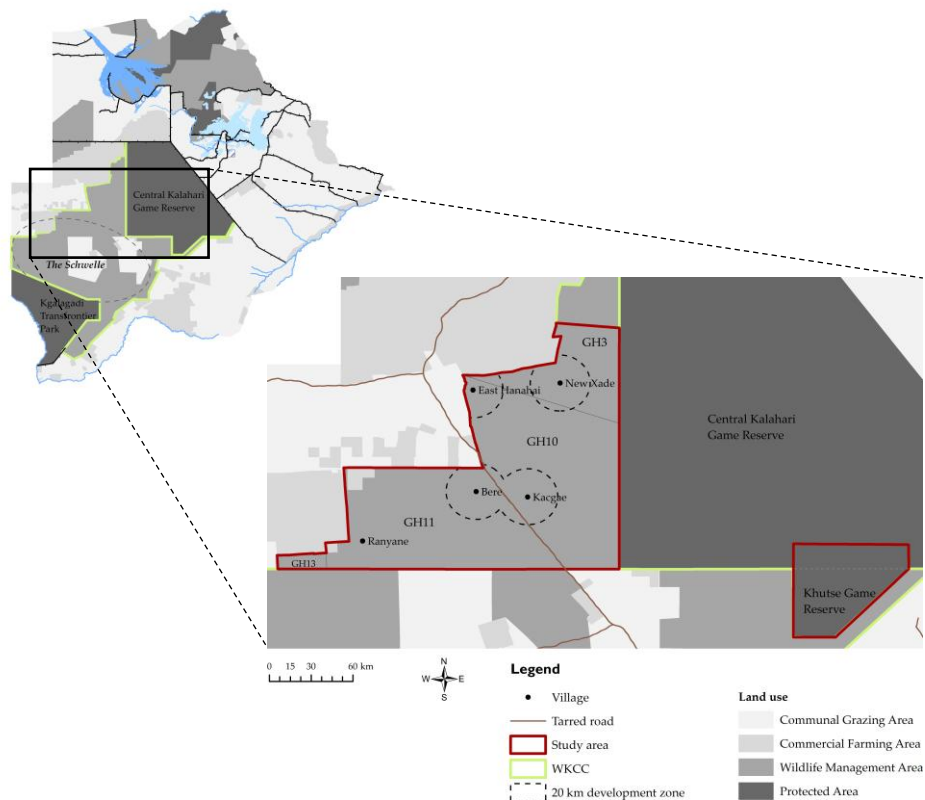


Figure 2-1 Study areas.

The first study area encompasses the WMAs “GH13”, “GH11”, “GH10” and south of “GH3”, adjacent to the CKGR and forming northern part of the WKCC. Dashed black line circles delimit the 20km development zones around WMA villages of the study area where inhabitants have developed cattleposts. Ranyane is not an official village, but rather an informal settlement that developed around a water resupply borehole. The second study area covers Khutse Game Reserve and an adjacent portion of the CKGR, with their shared unfenced boundary marked by a dashed green line.

Sampling units for track surveys were transects of varying lengths. In the northern part of the WKCC, the full transect pool used in Chapter 5 corresponds to nearly all accessible roads within the study area. This design aimed to maximise coverage and survey effort to improve the accuracy of wildlife density estimates, while accounting for the logistical constraint that off-road surveys were not feasible. The ideal transect distribution would have been randomised within a systematic grid, ensuring proportional sampling of local variations of wildlife habitat and, consequently, wildlife densities. However, this approach would have been prohibitively costly in this case. Nevertheless, the road network had a layout that allowed for sampling across gradients of various variables, such as distance to cattle posts, Commercial Farming Areas (CFAs) or certain pans, and different types of vegetation cover. This enabled to address several ecological questions, including characterizing the impact of environmental and anthropogenic factors on wildlife density, as well as identifying areas of highest densities and potential wildlife movement corridors. Chapter 3 uses a subset of the transect pool described above to address specific questions related to the impact of sampling conditions on the probability of track detection by observers. Finally, Chapter 4 utilises road transects designed by a third party as part of a long-term wildlife monitoring project, which also sample most of the accessible roads within Khutse Game Reserve and the adjacent portion of the CKGR. The detailed transect design and sampling periods for each study is described in the corresponding chapters.

4.2. Species

Wildlife data collection focused on key Kalahari species selected for their ecological importance, relevance to the tourism industry, and vulnerability to disturbance - typically large species. These species also leave more prominent tracks in the sand, making them particularly well-suited for study through track surveys. The entire community of large species (plus springbok, which is typically of medium size) present in Ghanzi WMAs was sampled, including six large carnivores and seven large herbivores, as illustrated in **Table 2-1** and **Table 2-2**). It should be noted that elephants have become increasingly present in the area. Although they were recorded casually, they were not included in the analyses due to the relatively recent nature of this development. Additionally, Chapter 4 incorporates four other herbivore species of interest: giraffe, warthog, duiker, and steenbok (**Table 2-3**).

Table 2-1: The six large carnivore species surveyed and their tracks (right front foot).

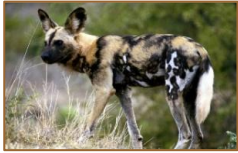
Species Name	Photographic illustration ¹⁻⁶	Track illustration (Liebenberg, 1990a)
African wild dog (<i>Lycaon pictus</i>)		
Brown hyena (<i>Hyena brunnea</i>)		
Cheetah (<i>Acinonyx jubatus</i>)		
Leopard (<i>Panthera pardus</i>)		
Lion (<i>Panthera leo</i>)		
Spotted hyena (<i>Crocota crocuta</i>)		

Image sources in display order:

¹<https://cdn.face2faceafrica.com/www/wp-content/uploads/2018/06/Wild-Republic.jpg>

²<https://i.pinimg.com/236x/3e/85/a6/3e85a60e9488f8d6988592d5ce1628f9--hyena-wild-animals.jpg>

³https://img.playbuzz.com/image/upload/ar_1.0,c_pad,f_jpg,b_auto/cdn/1d0eea41-c5a5-45be-9155-823e40adc364/0a6de016-2774-45b7-a1e2-07de2dd57e65.jpg

⁴<https://i.pinimg.com/originals/bd/84/df/bd84dfac4a2c128f21d7c87d611bc94f.jpg>

⁵<https://i.pinimg.com/736x/0c/5e/2f/0c5e2f3b5a886f4fc2b28c05454f9b5c--leo--march.jpg>

⁶<https://onekindplanet.org/wp-content/uploads/2017/06/iStock-147270142-1-e1503418484177.jpg>

Table 2-2: The seven large herbivore species surveyed and their tracks (right front foot).

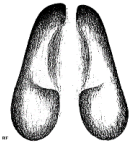
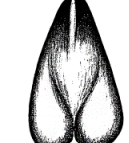
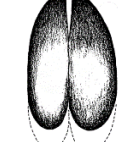
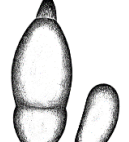
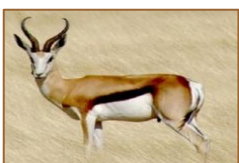
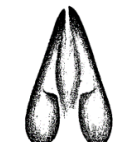
Species Name	Photographic illustration ¹⁻⁷	Track illustration (Liebenberg, 1990a)
Blue Wildebeest (<i>Connochaetes taurinus</i>)		
Eland (<i>Taurotragus oryx</i>)		
Gemsbok (<i>Oryx gazella</i>)		
Greater Kudu (<i>Tragelaphus strepsiceros</i>)		
Ostrich (<i>Struthio camelus</i>)		
Red Hartebeest (<i>Alcephalus buselaphus</i>)		
Springbok (<i>Antidorcas marsupialis</i>)		

Image sources in display order:

¹https://mydriase.fr/_data/i/upload/2019/09/03/20190903094947-6e26a5a9-la.jpg

²<https://www.numzaan.com/wp-content/uploads/2020/03/ELAND-CAPE.jpg>

³<https://static.wikia.nocookie.net/nickelodeon-movies/images/5/52/Gemsbok.jpg>

⁴<https://www.thakadubushcamp.com/wp-content/uploads/2017/01/kudu.jpg>

⁵<https://animalsadda.com/wp-content/uploads/2017/04/ostrich-10.jpg>

⁶<https://storage.cdn.bookyourhunt.com/images/d5b3d5cb-70a8-4388-874e-7df19bee208d/c32aeb4e-0cec-4fff-a3cd-c9932dd67bc7.jpg>

⁷By Coda.coza ([CC BY-SA 3.0](https://creativecommons.org/licenses/by-sa/3.0/)), https://upload.wikimedia.org/wikipedia/commons/thumb/6/65/Springbok_etosha.jpg/435px-Springbok_etosha.jpg

Table 2-3: The additional herbivore species surveyed in Chapter 4 and their tracks (right front foot).

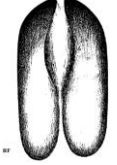
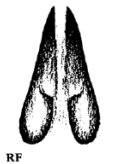
Species Name	Photographic illustration ¹⁻⁴	Track illustration (Liebenberg, 1990a)
Duiker <i>(Sylvicapra grimmia)</i>		
Giraffe <i>(Giraffa giraffa)</i>		
Steenbok <i>(Raphicerus campestris)</i>		
Warthog <i>(Phacochoerus africanus)</i>		

Image sources in display order:

¹<https://africanfieldsports.co.za/wp-content/uploads/2023/09/activity-grey-duiker.jpg>

²https://wildlifevagabond.com/wp-content/uploads/2023/08/IMG_4978-2-Edit.jpg

³By Yathin S Krishnappa ([CC BY-SA 3.0](https://creativecommons.org/licenses/by-sa/3.0/)), <https://commons.wikimedia.org/w/index.php?curid=24567648>

⁴By Charles J. Sharp ([CC BY-SA 4.0](https://creativecommons.org/licenses/by-sa/4.0/)) <https://commons.wikimedia.org/w/index.php?curid=55512532>

4.3. Equipment

Track surveys are relatively low-tech to perform, especially when conducted on foot or using animals like donkeys. However, in this study, vehicle-based sampling was preferred in order to cover the extensive area required within a reasonable time frame. Basic requirements in terms of equipment and field personnel consisted of (**Plate 2-3**):

- A 4x4 vehicle
- Tracker seats fitted in front of the bonnet
- A minimum of two skilled observers
- One driver and one recorder (who can be the same person)
- A data collection system, such as the CyberTracker App installed on a regular smartphone
- Optional radio transceivers



Plate 2-3 Track survey basic equipment.

The left photograph shows the 4x4 vehicle equipped with a roof tent and two tracker seats fitted on the front of the bonnet, where observers sit during the survey. The right photograph shows a data collecting team with their radio transceivers. From left to right: the two observers, the late Master tracker Horekhwe (Karo) Langwane and Master tracker Njoxlau Kashe, and myself as both the driver and recorder.

Photo credit: Nicolas Schtickzelle and Pierre du Plessis for the left and right photographs, respectively.

4.4. Observers

Eight certified trackers, assessed through the CyberTracker Tracker Certification program (Liebenberg et al., 2018), were employed from villages within the study areas to assist with the various studies directly associated with this thesis. An additional eight trackers conducted track surveys in Khutse Game Reserve as part of the Leopard Ecology & Conservation (LEC) research project, whose data are included in Chapter 4. Trackers usually work in groups of two or more to ensure cross-validation in the detection and identification of tracks.



Plate 2-4 The track survey team.

On the right photograph from left to right: myself as the driver and recorder, and the four trackers: Xiko Johannes, Glam Khumo, Zoro Zoronxhogo, and Njoxlau Kashe. On the left photograph: the late Horekhwe (Karohe) Langwane who assisted the 2019 and 2020 surveys as an observer.

Photo credit: Pierre du Plessis and Nicolas Schtickzelle for the left and right photographs, respectively.

In particular, track surveys in WMAs GH3/10/11/13 were assisted by five trackers (**Plate 2-4**). Their tracking certifications indicated below are based on the categories defined by Liebenberg et al.(2018):

- Xiko Johannes, Tracker III, from East Hanahai village (GH10).
- Zoro Zoronxhogo, Track & Sign I and Trailing III, from East Hanahai village (GH10).

- Njoxlau Kashe, Master tracker, from Bere village (GH11).
- Horekhwe (Karooha) Langwane, Master tracker, from Kacgae village (GH11).
- Glam Khumo, Tracker III, from Bere village (GH11), who replaced Horekhwe (Karooha) Langwane for the last two surveys in 2021 following his regrettable passing.

While the first two mostly surveyed GH3 and GH11, the last three focused on GH11 and GH13.



Plate 2-5 The trailing survey team.

From left to right: Alessandro Araldi (LEC Field Research Coordinator), Senxwai Mosololo (tracker), Seitshiro Pule (intern), myself, Duela Seganaphofu (tracker), Xee Fire Seganaphofu (tracker), and Marie Jardeaux (UCLouvain M.Sc. student).

Photo credit: Alessandro Araldi – Leopard Ecology & Conservation.

Trailing surveys (Chapter 4 only) were mainly assisted by three trackers (**Plate 2-5**):

- Senxwai Mosololo, Track & Sign III and Trailing Professional, from Kaudwane Village (KW4).
- Xee Fire Seganaphofu, Track & Sign III and Trailing Professional, from Kaudwane Village (KW4).
- Duela Seganaphofu, Tracker III, from Kaudwane Village (KW4).

4.5. Data collection following the Formozov-Malyshev-Pereleshin formula approach

The Formozov-Malyshev-Pereleshin (FMP) formula is a mathematical model developed in Russia nearly a century ago for estimating animal population density from track counts along transects. The formula is expressed as:

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

where, for a given species, the estimated counts of fresh (≤ 24 hours old) track interceptions ($\hat{x}$) with linear transects of total length S are converted into a population density estimate ($\hat{D}$) using the average estimated distance the animals travel in 24 hours ($\hat{M}$).

Conceptually, as an animal moves through the landscape, it leaves behind a trail of footprints, also referred to as tracks. If this trail intersects with one of the transects in its path, and conditions are suitable, the tracks will be visible along the transect. In the FMP theoretical spatial framework, both the animal trail and the transect are represented as one-dimensional elements (lines) that intersect at specific locations. These intersections are considered zero-dimensional points along the transect, referred to as “track interceptions.” Thus, during surveys, the data collected consist of all track interceptions along the transects for the species of interest. In practice, however, it is important to note that transects are two-dimensional (i.e. the space between vehicle wheels). This means that an entire segment of an animal's trail, rather than a single footprint, often intersects the transect. While several footprints from the same individual may be visible within this space, they are recorded as a single interception at one location (**Figure 2-2**).

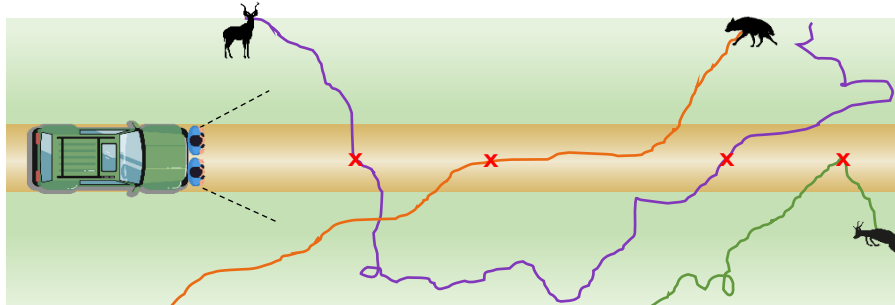


Figure 2-2. Illustration of data collection in driven track surveys.

The space bounded by the vehicle wheels (in sand colour) is theoretically summarised as a one-dimensional transect of length S , which intersects with the movement paths of animals in the landscape, each with an average length $\bar{M}$ over a 24-hour period. Each of their intersections appears as a series of footprints, called tracks, forming a trail on the transect. The trail segment of an individual who walk along the transect is counted as a single track interception (red x), regardless of the number of tracks it has left (e.g. brown hyena – orange 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 between the animal movement path and the transect (e.g. greater kudu – purple path). Figure adapted from Keeping et al. (2018).

Icon sources: car by Studioworkstock/Dreamstime.com, person by Nesterenkoruslan/Dreamstime.com, greater kudu by PxHere Team ([CC0 1.0](https://creativecommons.org/licenses/by/4.0/)), springbok by Miceking/Dreamstime.com, brown hyena from <https://africageographic.com>.

One observation unit during data collection is, therefore, a geolocated track interception by the transect. However, in some cases, animals travel in groups - such as certain large antelopes - creating a cluster of interlaced trails that cross the transect simultaneously (**Plate 2-6**). In such instances, the observation is not a single “individual animal track” interception but rather an “individual track set” interception. For this type of observation, the observers must distinguish the trail of each individual animal within the group to accurately count the number of individuals who made the tracks. For example, if five distinct trails are identified as belonging to five different individuals, the number of track interceptions recorded at that location would be five.



Plate 2-6 Trackers identifying the interlacing trails of two individual lions on a transect.

Photo credit : Jess Isden. Photo taken during a Tracking Training Workshop co-created by LEC and Marie-Charlotte Gielen and hosted by WildCRU and DWNP.

In terms of survey design and protocol, the FMP formula approach requires three assumptions to be met (Keeping & Pelletier, 2014):

1. **Animal movements are independent of transect placement.** This implies that naturally non-random animal movements are not influenced by the presence of a transect. In terms of transect design, this means that transect must not serve as a feature that either attracts or repels the species of interest.
2. **All animals that intersect transects are detected and identified correctly.** In practice, this requires ensuring optimal survey conditions as much as possible, such as:
 - Observers (trackers) must possess excellent tracking skills to accurately detect and identify tracks. Ideally, more than one tracker

should be present in order to maximise detection and minimise errors in track identification.

- Driving speed must not exceed 10km h⁻¹ - the average cruising running speed for a human - to reduce the risk of missing tracks. When necessary, trackers may request the driver to slow down to adapt to the visibility of the transect. In cases of uncertainty regarding track detection or identification, or when counting individual animals from a large track set interception, trackers instruct the driver to stop the vehicle so they can examine the tracks on foot.
- Trackers are seated on specially designed seats fitted to the bull bar at the front of the 4x4 vehicle, approximately 1 meter above the ground, providing them with an open and wide view of the substrate (**Plate 2-7**). Additional trackers may also observe from the vehicle rooftop. Trackers focus their attention on the sand strip between the vehicle wheels, which defines the transect width. When visibility extends beyond the transect, trackers commonly make use of the open space on either side to visually detect animal trails more easily before they cross the transect and are recorded.



Plate 2-7 Example of a transect.

A pair of trackers, Njoxlau Kashe and Horekhwe (Karo) Langwane, are seated on the tracker seats, scanning the transect sand for tracks as the vehicle moves during data collection.

Photo credit: Marie-Charlotte Gielen

- Surveys must be conducted during daylight hours when track visibility is optimal, avoiding midday periods when the lack of shadows makes track depressions harder to detect against the surrounding terrain.

- If environmental conditions completely erase tracks on the transect (e.g. heavy rain and wind), a minimum of 24h must pass before resuming the survey to allow new tracks to imprint on the substrate and be collected as fresh tracks (≤ 24 h hours old).
 - If logistical means allow it, transects can be smoothed out (e.g., with tyres dragged behind a vehicle) 24 hours prior to the survey to improve visibility and ensure that all tracks collected are ≤ 24 hours old. If older tracks need to be included, the transects should not be dragged or should be dragged at an appropriate time before the survey to match the track age of interest (e.g., 1 week prior if the tracks of interest are up to 1 week old).
3. **All intersections are enumerated regardless of individuals' identity.** As the FMP formula operates as a random encounter model between two lines in space (i.e. the transect and the animal movement path), multiple re-crossings by the same individual animal must be recorded. However, exceptions are made when the animal is visibly walking along the transect (creating an uninterrupted trail) or drifts away from it for short distances before returning. In such cases, the animal's path is no longer considered random as it is actively following the transect, and track interceptions are not recounted.

In relation to these assumptions, it seems appropriate to briefly introduce the concept of **track detectability**, which forms a central theme of the research presented in Chapter 3 and 4. Two processes influence the number of tracks detected along a transect at any given point in time. The first is biological, referring to the characteristics of the species itself, which I term the *individual animal detectability* or $\hat{p}_1$. In other words, this is the *probability that animal movement paths intersect with the sampling unit at least once*, so that tracks are left to be recorded. This probability is indirectly incorporated into the FMP formula through all its parameters. For a given population size within the study area, the total transect length S , the species' average daily travel distance estimate $\bar{M}$, and the random nature of their intersection (related to $\frac{\pi}{2}$) determine the number of track interceptions (x) left on the transect. It is important to note that the tortuosity of the animals' daily paths does not affect x : "individuals with more tortuous movements are detected less but, when encountered, those individuals are generally counted a larger number of times by virtue of the convoluted pattern of their movement" (Keeping & Pelletier, 2014). Therefore, it is critical to count every track interception along the transects regardless of individuals' identity (Assumption 3). It is also

essential that $\hat{p}_1$, which applies to a random encounter scenario, remains unbiased by attraction to or avoidance of transects in order to yield accurate density estimates (Assumption 1). The second detectability component pertains to the sampling process and its conditions, which defines the *probability of track detection* or $\hat{p}_2$. This is 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, substrate type, alteration by disturbance factors). Accurate density estimates can only be obtained if $\hat{p}_2$ is measured or can be assumed to be equal to one (Assumption 2). Algebraically, we can present the FMP equation under the light of its two detectability components as follows:

$$\hat{D} = \frac{\pi \cdot \hat{x}}{2 \cdot S \cdot \hat{M}} = \frac{y}{A \cdot \hat{p}_1 \cdot \hat{p}_2}$$

where A is the study area of size and y is the number of animals (amongst the total population present in A) crossing S, at least one time. Further details on track detectability in relation to the FMP formula are provided in the introduction of Chapter 3 and 4, as well as in **Appendix 4A**.

In terms of data collection, for each observation unit intercepting the transect, the following minimum information should be collected:

- Date and time
- GPS location
- Name of the transect
- Name of the species
- Number of individual animals (i.e. 1 for an individual animal track interception, and the exact number of animals for an individual track set interception)
- Time elapsed since the track imprinted (i.e. age of track)
 - ≤24h
 - 2 days
 - 3 days
 - 3 days +, i.e. 3-6 days
 - 1 week +, i.e. 7-30 days
 - 1 month +, i.e. 1 month or older.

As noted by Liebenberg (1990b), estimating track age is one of the most challenging aspects of tracking, due to the many variables involved. Even for

highly experienced trackers, age estimation is often intuitive at best. The accuracy of track age determination is most reliable for tracks ≤ 24 hours old, with accuracy decreasing exponentially as track age increases. The primary objective here is to differentiate tracks that are ≤ 24 hours old from older tracks. The former is used in animal density estimation (Chapters 4 and 5), while the latter may also be incorporated into analyses of animal density distribution or movement corridors (Chapter 5). Additionally, the age of older tracks was used to compare and match track pools collected by different tracking teams, in order to assess the probability of track detection by observers (Chapter 3).

For each transect, the effective driven length is also recorded as a parameter in the FMP formula, typically using a handheld GPS. The total transect length S , which is the sum of each individual transect length, is used to calculate the estimate of density. The individual transect lengths are then used to calculate the confidence intervals around this estimate (see more details in the following chapters).

4.6. The CyberTracker application

Track data can easily be recorded using the [CyberTracker](https://cybertracker.org/) application on a smart phone (**Figure 2-3**). Developed in 1996, it was originally designed for illiterate trackers with an Icon User Interface that enable expert oralate trackers to record complex geo-referenced data on animal behaviour (Liebenberg et al., 2017). Since then, it has proven invaluable in large-scale, long-term monitoring of ecosystems for conservation management (Ahlsweide et al., 2019; Keeping, Burger, et al., 2018; Liebenberg et al., 2017). Beyond such use, CyberTracker is now being used worldwide by Indigenous communities, in Protected Areas, scientific research, tracking science, citizen science, environmental education, forestry, farming, and even social surveys and crime prevention (<https://cybertracker.org/>).

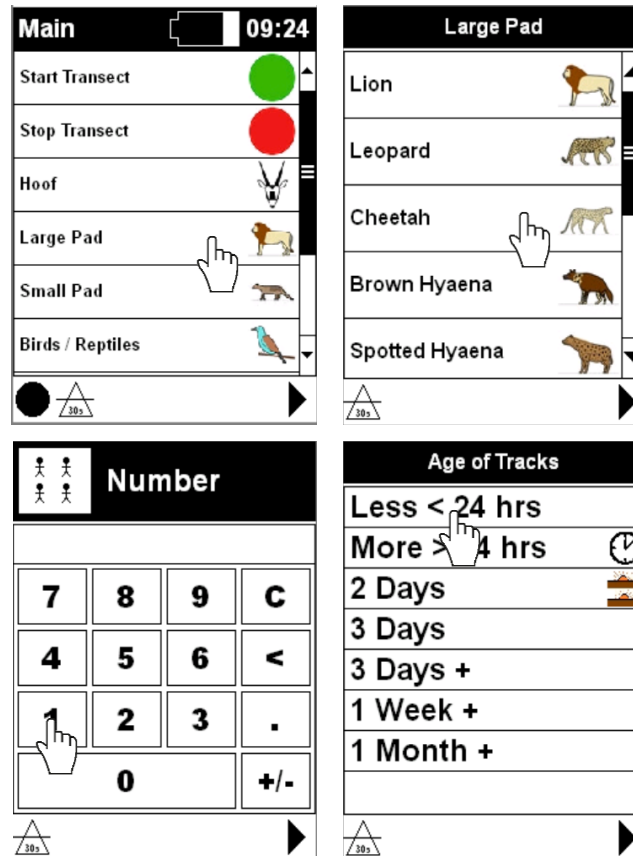


Figure 2-3 Example of the succession of Icon User Interface designs in CyberTracker, used for data entry during the track surveys.

The CyberTracker desktop software, and the new CyberTracker Online, allows to customise one's own CyberTracker application so it meets data collection needs of various sectors. The smartphone interface is particularly user-friendly, enabling significantly faster data collection compared with text-based interfaces or written methods. It also reduces data input and re-transcription errors. **Appendix 4C** and **Appendix 5A** provide detailed examples of the CyberTracker application used for track surveys and trailing surveys, which are part of this thesis.

Once the track survey is completed, the data are automatically uploaded from the smartphone to a computer equipped with the CyberTracker desktop software (as used during the time of this thesis). From there, the data can be exported into ready-to-use spreadsheets (**Figure 2-4**).

	A	B	C	D	E	F	G	H	I	J	K	L
1	Date	Time	Latitude	Longitude	Accuracy	Transect	Names of Trackers	RecType	Species	Number	Track Age	Note
2	02-05-19	10:50:27	-22,167395	21,8822995		0,3 Hanahai - Okwa Valley	Xiko and Zoro	Large Pad	Brown Hyaena		1 Less < 24 hrs	
3	02-05-19	11:12:47	-22,161775	21,9189313		0,3 Hanahai - Okwa Valley	Xiko and Zoro	Hoof	Kudu		1 1 Week +	
4	02-05-19	11:16:19	-22,164952	21,9242285		0,3 Hanahai - Okwa Valley	Xiko and Zoro	Large Pad	Leopard		1 Less < 24 hrs	
5	02-05-19	11:34:30	-22,18148	21,9525069		0,3 Hanahai - Okwa Valley	Xiko and Zoro	Hoof	Kudu		1 Less < 24 hrs	
6	02-05-19	11:56:01	-22,200932	21,9862587		0,3 Hanahai - Okwa Valley	Xiko and Zoro	Large Pad	Brown Hyaena		1 Less < 24 hrs	
7	02-05-19	11:57:30	-22,201908	21,9881048		0,3 Hanahai - Okwa Valley	Xiko and Zoro	Hoof	Gemsbok		1 Less < 24 hrs	
8	02-05-19	12:34:48	-22,245752	22,0374672		0,3 Hanahai - Okwa Valley	Xiko and Zoro	Large Pad	Wild Dog		1 Less < 24 hrs	
9	02-05-19	15:24:10	-22,404734	22,0823154		0,3 Okwa Valley East	Xiko and Zoro	Large Pad	Leopard		1 1 Week +	
10	02-05-19	15:25:07	-22,404503	22,0829322		0,3 Okwa Valley East	Xiko and Zoro	Hoof	Gemsbok		1 Less < 24 hrs	
11	02-05-19	15:25:47	-22,404424	22,0834816		0,3 Okwa Valley East	Xiko and Zoro	Hoof	Kudu		1 Less < 24 hrs	

Figure 2-4 Example of a spreadsheet exported from the CyberTracker desktop software where track data entries are automatically organised.