Université catholique de Louvain
Ecole de Biologie

Université de Namur
Département de biologie

Leopard Ecology & Conservation

# Quantification of daily travel distance for five large herbivore species as a prerequisite to estimate their population abundance in Botswana

Jardeaux Marie

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Main supervisor : Prof. Nicolas Schtickzelle (UCLouvain)
Advisors : Marie-Charlotte Gielen (UCLouvain, Leopard Ecology & Conservation, and Cheetah Conservation Botswana) / Alessandro Araldi (Leopard Ecology & Conservation)

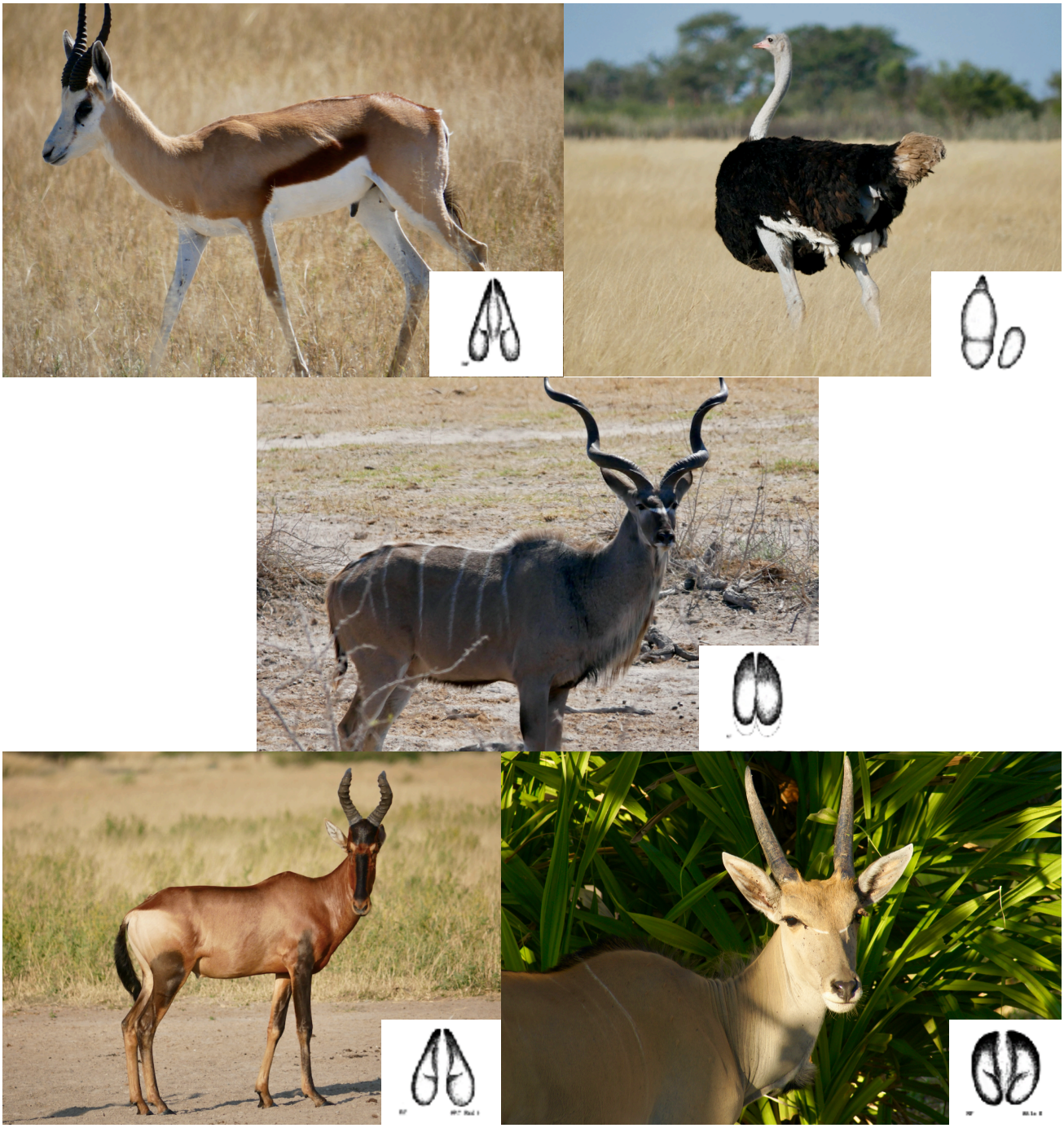

Photo credit : Marie Jardeaux
Animal tracks retrieved from Liebenberg (1990a)

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Pictured of the field team. From left to right : Alessandro Araldi, Senxwai Mosololo, Seitshiro Pule, Marie-Charlotte Gielen, Duela Seganaphofu, Xee Fire Seganaphohu and myself (Marie Jardeaux).

# Content

# Abstract

The Kalahari Desert is a source of great biodiversity, threatened by human activities. To mitigate anthropogenic pressures, conservation programs have been set up. In order for these programs to be as effective as possible, some key parameters must be known. One of these is the population density of the species targeted by conservation efforts. Although there are various methods for calculating species population densities, track surveys present several advantages in the Kalahari Desert. Indeed, thanks to its sandy substrate and the ability of some local trackers to read animal tracks as easily as we can read a book, track surveys are a promising technique. One analytical approach to track surveys is the Formozov-Malyshev-Pereleshin (FMP) formula. For the purposes of this master's thesis, we are focusing on this method.
However, the main limitation of this technique is its parameter $\hat{M}$, which corresponds to the average daily travel distance (DTD) estimate of the species studied. The best estimate comes from empirical data, i.e. calculated from field observations, collected in the study area. When unavailable, this distance is estimated allometrically, i.e. it has been calculated using a relationship between the average body mass of the species studied and the average DTD estimate. However, in the Kalahari, for a same species, when the average allometric DTD estimate is compared with the empirical estimate, the empirical estimate is often higher than the allometric one. This difference therefore affects the final population density estimate for the species studied.

This master's thesis, therefore, focuses on collecting average empirical DTD estimates for five species with allometric values only. We studied eland (*Taurotragus oryx*), greater kudu (*Tragelaphus strepsiceros*), red hartebeest (*Alcelaphus buselaphus*), springbok (*Antidorcas marsupialis*) and ostrich (*Struthio camelus*). To obtain these data, we used a long-follow trailing method during three months in the cold dry season 2023. We collected 61 exploitable trails all species combined, and obtained the following average DTD estimates : eland 10.468 km, greater kudu 5.842 km, red hartebeest 5.843 km, springbok 1.790 km and ostrich 5.155 km. For four of the five species (eland, greater kudu, red hartebeest and ostrich), the empirical value is greater than the allometric value. The springbok's empirical value is smaller than its allometric value.
With these new empirical data and the data found in the literature on other Kalahari species, we have created a correction coefficient that can be applied directly to the allometric values. This enabled us to obtain a more accurate average DTD estimate for species for which no empirical value exists.
Finally, using demographic data collected on the animals trailed, we assessed how group size, sex and social structure could influence the DTD. We also assessed if the DTD increased or decreased throughout the cold dry season. The results were inconclusive, but this may be due to the small sample size.

The results of this study will enable us to obtain more accurate population densities, via the FMP formula, for our five species in the region. This could ultimately allow better informed conservation decision towards these species in the Kalahari Desert. To collect empirical DTD, the long-follow trailing method has proved highly effective, and also helps to highlights the rare abilities of trackers and helps to preserve them.

# Résumé

Le Désert du Kalahari est source d'une grande biodiversité menacée par les activités humaines. Pour atténuer les pressions anthropiques, des programmes de conservation sont mis en place. Afin que ces derniers soient les plus efficaces possibles, certains paramètres clés doivent être connus. L'un d'eux est la densité de population de l'espèce ciblée par les programmes de conservation. Bien qu'il existe différentes méthodes permettant de calculer les densité de populations, les « track surveys » présentent plusieurs avantages dans le Désert du Kalahari. En effet, grâce à son substrat, le sable, et les capacités de certains trackers pouvant lire les traces des animaux aussi facilement que nous pourrions lire un livre, les « track surveys » sont une technique prometteuse. L'une des approches analytiques des « track surveys » est la formule Formozov-Malyshev-Pereleshin (FMP). Dans le cadre de ce mémoire, nous nous concentrons sur cette méthode.
Pourtant, cette technique possède une limitation principale est le paramètre $\hat{M}$, qui correspond à l'estimation de la distance parcourue quotidiennement (DPQ) moyenne de l'espèce étudiée. La meilleure estimation est une valeur empirique, c'est-à-dire calculée grâce à des observations faites sur le terrain, collectée dans la zone d'étude. Quand cette valeur n'est pas disponible, elle est estimée de manière allométrique, c'est-à-dire qu'elle a été calculée à l'aide d'une relation entre la masse corporelle moyenne de l'espèce étudiée et l'estimation de sa DPQ moyenne. Or, dans le Kalahari, pour une même espèce, lorsque la DPQ moyenne allométrique est comparée à l'estimation empirique, la valeur empirique est souvent supérieure à l'allométrique. Cette différence ce répercute donc sur l'estimation finale de la densité de population de l'espèce étudiée.

Ce mémoire se concentre donc sur collecter des estimations empiriques de la DPQ moyennes pour cinq espèces possédant uniquement des valeurs allométriques. Nous avons étudié l'éland (*Taurotragus oryx*), le grand koudou (*Tragelaphus strepsiceros*), le bubale roux (*Alcelaphus buselaphus*), le springbok (*Antidorcas marsupialis*) et l'autruche (*Struthio camelus*). Pour obtenir ces données, nous avons utilisé la méthode des « long-follow trailing » pendant trois mois en pleine saison sèche 2023. Nous avons collecté 61 traces exploitables toutes espèces confondues, et obtenu les estimations des DPQ moyennes suivantes : pour l'éland 10,468 km, pour le grand koudou 5,842 km, pour le bubale roux 5,843 km, pour le springbok 1,790 km et pour l'autruche 5,155 km. Pour quatre des cinq espèces (l'éland, le grand koudou, le bubale roux et l'autruche), la valeur empirique est plus grande que la valeur allométrique. La valeur empirique du springbok, quant à elle, est plus petite que sa valeur allométrique.
Avec ces nouvelles données empiriques et les données trouvées dans la littérature sur d'autres espèces du Kalahari, nous avons créé un coefficient correcteur pouvant être appliqué directement sur les valeurs allométriques. Cela nous a permis d'obtenir une DPQ moyenne plus précise pour les espèces ne possédant pas de valeur empirique.
Enfin, à l'aide des données démographiques collectées sur les animaux suivis, nous avons évalué comment la taille du groupe, le sexe et la structure sociale pouvaient influencer les DPQ. Nous avons également évalué la DPQ augmentait ou diminuait au cours de la saison sèche. Les résultats obtenus n'ont pas été concluants mais cela pourrait être dû à une taille d'échantillon trop petite.

Les résultats de cette étude vont permettre d'obtenir des densités de population plus précises, via la formuleFMP, pour nos cinq espèces dans la région. Cela pourrait permettre, au final, des décisions de conservation plus éclairées pour ces espèces dans le Désert du Kalahari. Pour collecter les DPQ empiriques, la méthode des long-follow trailing s'est révélée très efficace et permet également de mettre en lumière les capacités rares des trackers et d'aider à les préserver.

# I. Introduction

We are currently facing two urgent, and intrinsically linked, problems caused by human activities : climate change and the loss of biodiversity. In a world with limited resources and a growing human population, the nature is under pressure from human activities (industry, land consumption, intensive agriculture, etc.). The loss of biodiversity, i.e. the extinction of animal and plant species throughout the world and the disappearance of ecosystems, is a process that has always occurred in the history of our planet (Elewa and al. 2020). Yet, today, the rate of extinction is unprecedented and continues to accelerate (United Nations Environment Programme - UNEP, 2019). Reports such as the ones by IPBES ("The Global Assessment Report on Biodiversity and Ecosystem Services", 2019) or the WWF ("Living Planet Report 2022", 2022) show us that all the lights are red. These are alarming conclusions, especially as we just begin to understand the fundamental role played by biodiversity in our health (e.g. Covid 19 pandemic (Roche and al., 2022)), ecosystem productivity (Isbell and al., 2013) and the stability of many natural systems (Hautier and al., 2015) on which depends every life on Earth, including our own. As we start to recognize the need for safeguarding our beloved blue planet, and consequently, our own existence, the importance of protecting nature is finally becoming acknowledged.

Among all continents, Africa is home to remarkable biodiversity (Myers, 1988; Myers et al., 2000; Brooks et al., 2002; Tschakert et al. 2022). It has the most intact collection of large terrestrial mammals (UNEP-WCMC, 2016), including iconic species such as lions (*Panthera leo*), giraffes (*Giraffa camelopardalis*), elephants (*Loxodonta africana*), leopards (*Panthera pardus*), gemsboks (*Oryx gazella*), wildebeest (*Connochaetes taurinus*), or wild dogs (*Lycaon pictus*). However, as in the rest of the world, African flora and fauna are under increasing pressure. Human population growth, livestock farming, unsustainable exploitation of resources (e.g. fisheries, water consumption, land consumption, mining), poaching, invasive species, deforestation and climate change are some of the causes of the loss of this biodiversity (Vijeta et al., 2021; Wood et al. 2013). Every country faces a number of environmental challenges caused by human activity (Darkoh, 2009). These different challenges are often interlinked, for example the increase in human population leading to a need for additional land to cultivate and therefore to deforestation. In Botswana, for example, one of the main environmental challenges is livestock farming. In this country, livestock is enclosed in fenced farms only in Commercial Farming Areas and are free-ranging in Communal Grazing Areas. In the latter cattle often roam freely the bush and return to

drink at the cattleposts[1] when they need. Population growth in Botswana has led to an increase of cattle population in both Commercial Farming Areas and Communal Grazing Areas (Darkoh and Mbaiwa, 2002). As a result, more wild lands have been converted to raise cows, which has led some of them to degradation through overgrazing. At present, however, of the two types of livestock farming mentioned above, uncontrolled livestock farming in communal grazing land is probably the biggest threat to the remaining wild ecosystems. One issue is that, most of the time, cattle are not herded. There are several consequences of the lack of surveillance of herds. Firstly, livestock can go far from their original cattle post and often encroach on Wildlife Management Areas[2] or protected areas. The lack of herding can also increase conflicts with wild animals, particularly large predators (lions, leopards, etc.) who may see them as easy preys. Another potential problem is competition for food between farmed and wild animals (Young et al., 2005). Livestock can graze around the reserves. But, the areas around protected areas are important buffers to keep healthy wildlife populations. In fact, they not only maintain the space between the farming areas and the protected zones, but also create corridors for animals where they can find key resources. In addition, corridors help to keep different protected areas connected, and the conservation of connectivity is crucial for long-term viability of wild populations. In this scenario, monitoring wildlife population trends is essential to detect when anthropogenic pressures threaten the long-term survival of wild animal populations.

Many conservation and management programs, in the world, have been developed in an attempt to remedy to the biodiversity loss : creation of nature reserves (Wu and al., 2011), creation of corridors (Bonnin, 2006), better forest management (Frehner and al., 2005), reduction of light pollution (Siblet, 2008), etc. However, creating and monitoring such programs require several questions to be answered, such as "How many individuals of this species are there ?", "Is the population increasing or decreasing?". To answer these questions, one key parameter, needs to be estimated : population abundance, or population density when expressed per unit of area.

Estimating the abundance of individuals of a species, is necessary to generate quantitative figures such as an estimate of 42,100 endangered species worldwide (IUCN, 2023). These figures help to assess the need of a protection program or species management plan and define their level of resource allocation (Datta et al., 2008; Nislow et al., 2011). Population abundance estimates can

[1] One or more wooden enclosures with huts for the sheperds and a water point supplied by groundwater (Perkins, 1996).

[2] Area where wildlife utilisation is to be the primary form of land use (Parry and Campbell, 1990)

also be linked to environmental variables to identify factors impacting species populations (Fahrig et al., 2009). Monitoring population abundance over time is also necessary to assess the effectiveness of conservation efforts and understand how species respond to them (Nichols, 2014), adjust fishing (Sancho and Mitchell, 1975) or hunting quotas (Peeters and al., 2022) to mention a few examples.

## 1) Estimating population density

When we think of "calculating the population abundance of a species", i.e. to know the number of individuals in a given area, we may think of counting all the individuals in the study area. We would therefore like to carry out a complete census of the population. Unfortunately, the situations in which a complete census is possible are rare, likely only applicable to small populations living in a restricted area. Solutions have therefore been put in place to estimate the number of individuals in a population from partial counts, rather than counting them all. As such, partial counts usually involve selecting sampling units across the study area and counting the number of individuals (or the signs) of the target species found in them.

Estimating population density from partial counts is a very broad concept, bringing together a long list of methods that must be chosen according to different criteria. Indeed, each method has its advantages and disadvantages, and these must be considered when designing a study. Not just any technique can be used, depending on the mobility of the organism (e.g. animals versus plants), the target species, field and climatic conditions, or budget (Seber, 1986; Schwarz, 1999).

One of the methods we can use to count the number of individuals is the capture-mark-recapture method (Nichols, 1992; Schwarz and Arnason, 1996). Taking bats as an example, large nets are strategically positioned to trap the animals. Each animal captured is counted and marked (in this case with rings adapted to the size of the species). The individual is then released. The number of captured individuals that have already been tagged during a previous capture will be recorded, as well as the number of individuals captured for the first time. A formula then allows us to estimate the number of individuals in the population, using the number of animals already tagged and those that were not. (Bart, 1995; Nichols, 1992).

However, you don't always have to see animals with your own eyes. Fortunately, because many species are difficult to see, whether it is because of their size, the environment in which their live, their behaviour, or the difficulty to mark them.

Some species produce sounds that are easily identifiable and can be used to estimate the population density of the species. Acoustic observations can be made in a variety of environments, both terrestrial and aquatic.

In dense forest or in the ocean, the passive acoustics method consists of placing a self-contained recorder that will record all the sounds it picks up within a specific time period. Once the recorder is retrieved, the sounds are analyzed (manually or automatically using software) (Marques et al. 2012). Most of the time, it is not possible to identify the single individuals from the recordings. Formulas have therefore been developed that relates the number of vocalisations detected, the proportion of detections that are false positives, the surface area of detection, the probability of detection in the zone and a multiplier (Marques et al. 2012). This equation will give an estimate of the population density. This method has, for example, been used with elephants in Ghana (Thompson et al. 2010).

Others techniques use indirect signs (tracks, droppings, dens, etc.) that indicate the presence of organisms in the environment (Keeping and Pelletier, 2014). For any wildlife monitoring technique, whether using direct or indirect signs, the probability of detecting the species (i.e. its detectability) is the key parameter to convert the number of observations in an estimate of the number of individuals present. The detectability function gives an idea of the probability of observing the target species in the sampling unit. In most situations, this probability decreases as the observation distance increases. The detectability function therefore corrects the population densities calculated for all the individuals that the observers may not have seen during sampling (Ramsey and Harrison, 2004).

If the detectability of the target species has been measured, the absolute abundance of the population can be obtained. In other words, we can estimate the number of individuals the studied population comprises. If detectability has not been measured, but is simply assumed constant, only relative abundance or an index can be obtained. So, we can infer whether our population is increasing or decreasing over a given time period, but we cannot estimate the absolute number of individuals.

## 2) The case of large wildlife species in the Kalahari

As mentioned above, the target species and the environment in which it lives will narrow the range of techniques that can be used to estimate its population abundance. In the case of this thesis, the target species are the large herbivores living in the Kalahari, a gigantic semi-arid sandy region in southern Africa (Grove, 1969). We are, therefore, dealing with a situation where a complete census is not achievable.

To calculate an estimate of the abundance of several large herbivore populations in this type of environment, we need a method that meets several conditions. It must allow us to sample a range of different species simultaneously with the same accuracy, to detect species with a relatively low population density characteristic of the Kalahari, and to cover a large study area.
Several methods could be used to estimate species population abundance in such case.

A first one is aerial counts. For this method, the study area is divided in several stratums. Every stratum is characterized by similar features such as habitat type, vegetation density, or other ecological factors. Enough strip transects are deployed according to the percentage of each stratum across the entire study area. During the survey, a plane with at least 2 observers flies over the strip transects at a height of between 100 and 150m. The observers count all the individuals of the target species they see within the strip transect width. Then, the number of individuals is divided by the area sampled for each stratum, producing density index per stratum. Successively the overall abundances of the species in the study area can be extrapolated according to the percentage of each stratum across the study area. This provides estimates of densities within each stratum which can be combined to provide an overall estimate for the survey area (Norton-Griffiths,1978; CITES MIKE Programme, 2020; Jolly, 1969).
However, aerial counts are subject to detection and counting bias. Indeed, animal detection can be influenced by the vegetation density (e.g. the bush can be dense in the Kalahari, so it is more difficult to see them), the size and color of the animals (e.g. the species we study, such as greater kudu, are very easily camouflaged in the vegetation, which can make them very difficult to spot from the air), the group size, the reaction of the animals to an over-flying aircraft, the light conditions and the weather (Jachmann, 2002). Finally, this method is very expensive.

A second technique for population abundance estimation is distance sampling along line transects, also known as distance sampling. This technique involves moving along transects of given length (L) place at random within an area of known size. During this time, the observers look for animals. Once an animal has been spotted, it will be recorded, along with other measurements : the spotting distance (r), i.e. the distance between the observer (O) and the animal (P) at the moment when the animal was seen, the sighting angle (θ) (i.e. the angle between the transect line and the sighting line), and the perpendicular distance (x) between the transect and the animal (generally derived by r and the angle, if you are driving line transects) (Figure 1). These parameters allow to calculate the probability of detecting an animal. This probability decreases as the distance of the animal from the transect increases. A formula is then used to link the number of individuals per species seen, the length of the transect and the probability of detection to obtain an estimate of population density (Jachmann, 2002, Burnham et al., 1980).

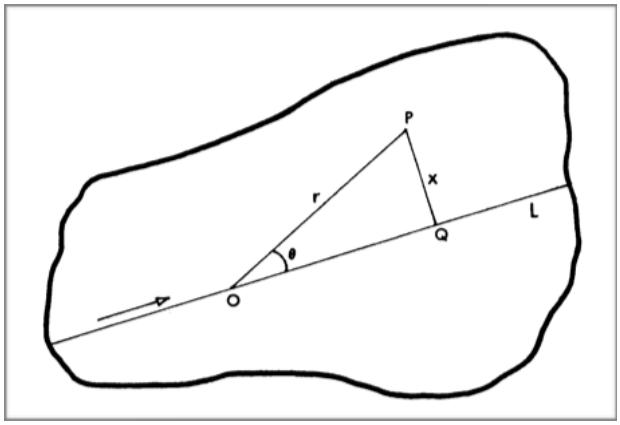


**Figure 1 : Representation of the masures necessary when observers find an animal (Burnham et al., 1980)**

However, this method requires a minimum number of observations necessary for fitting the detection function. Because of the low population density of the species present in the Kalahari, large transect lengths would be needed to obtain a sufficient number of observations. From a logistical point of view, however, transects of this size are complicated to carry out (Keeping et al., 2018). Therefore, the use of ground line transects in such an environment may not be optimal.

Another method is photographic traps. Cameras are positioned in strategic locations on immobile objects (tree, poles, etc.). Strategic locations are for instance areas of regular animal passage (e.g. game trails, waterholes, etc.). When a location like this is found, researchers clean out the grass and little branches in front of the camera, which will prevent the camera from being triggered by the movement of grass and give better visibility of the photos taken. Thanks to an infra-red motion sensor, the animals that pass in front of the camera are photographed. Additionally, according to estimation methods, some parameters need to be measured in order to use the photos for generating an abundance estimate for the target species. For example, the formula by Rowcliffe et al. (2008)

requires the trapping rate (the number of photos per unit of time), the species speed of movement and the dimension of the camera detection zone. These parameters contribute to measure the detectability of the target species (Rowcliffe et al., 2008).
When the study area is large and remote, camera trap techniques may present some limitations related to initial and maintenance costs, as well as issues related to theft or damage by animals or people, which can quickly become unsustainable. Hot climatic conditions in the Kalahari also increase camera failure (Apps et al., 2018). Therefore, camera trapping may not be the most suitable technique for abundance estimation in the Kalahari unless the project resources are high.

On the other hand, an interesting method for monitoring mammal abundance in the Kalahari is track (i.e. animal footprint) counts along transects. This method consists of counting, along transects of given length, the intersections between the animal movement paths and the transects as the number of track interceptions over a given time period.
There are various approaches to convert the number of track interceptions into density estimates that can be used next. For examples, the Formozov-Malyshev-Pereleshin (FMP) formula (Stephens et al., 2006, Keeping, 2014), or the Funston et al. (2010) regression.
Counting tracks meets all the following requirements. Both large and small animals can be counted, as long as their footprints are imprinted on the substrate (in this case, sand). This method can cover a large area, while collecting a higher number of data for a lower cost compared to other methods (Seidlitz et al., 2021; Keeping et al., 2018; Stephens et al., 2006). This technique has another advantage: it has low ecological impact if done along existing roads.
From each footprint found on the transect, information such as the species, sex, animal age-class, and track freshness can be collected.

Nevertheless, track surveys have several assumptions to be met to produce reliable estimates. The first one is the availability of a suitable substrate for tracks to imprint (e.g., sand, mud, dust, snow), which is met in the Kalahari as covered by sand. The second one is to detect and identify tracks correctly, which needs observers with high levels of tracking skills. This is the case of some local inhabitants who are known to be highly skilled trackers. Collaborating with local Indigenous trackers is beneficial for both parties. For researchers, it ensures accuracy of track identifications. For the local communities, it allows some of their members to be involved in and benefit from species conservation projects and to preserve their knowledge.

## 3) Track survey - the Formozov-Malyshev-Pereleshin formula

To convert track counts into population density, the Formozov-Malyshev-Pereleshin (FMP) formula is a promising solution (Stephens et al., 2006). This method has been used for a long time in Russia (Formozov, 1932), and adapted a decade ago to the Kalahari (Keeping, 2014), where it has been applied by several studies and validated against other widely practiced methods for wildlife population monitoring such as line transects or aerial counts (Keeping et al., 2018, Ahlswede et al., 2019, Romani et al., 2018).

The FMP formula consists in a random encounter model based on the probabilistic intersection (track encounter) of lines of known length (transect and animal movement path) within a known area (Stephens, 2006 ; Keeping, 2014). In other words, it uses an estimate of the species average daily travel distance to estimate the species density from its track (fresh for a maximum of 24 hours) counts on defined transects.

So, once the data have been collected, this index (the number of track interceptions per transect length) is converted into the absolute abundance thanks to one parameter : the daily travel distance (DTD) as followed :

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

$\widehat{D}$ : the species population density estimate
x : the total number of track interceptions by the total transect lengh over one 24h period
S : the total transect length
$\widehat{M}$ : the average daily travel distance (DTD) estimate for the species in the study area

In Eq.1, the parameters $\pi/2$, S et $\hat{M}$ relatively to x allow us to intrinsically measure the detectability of the animals. The advantage of measuring the probability of detecting animals is that we can obtain the absolute abundance of the population of the target species. Indeed, counting track

interceptions per transect length alone can only give us a relative estimate of population density, if the track detectability can be assumed constant.

Once the population density has been obtained, it is possible to obtain the number of individuals of the target species by multiplying the density by the study area.

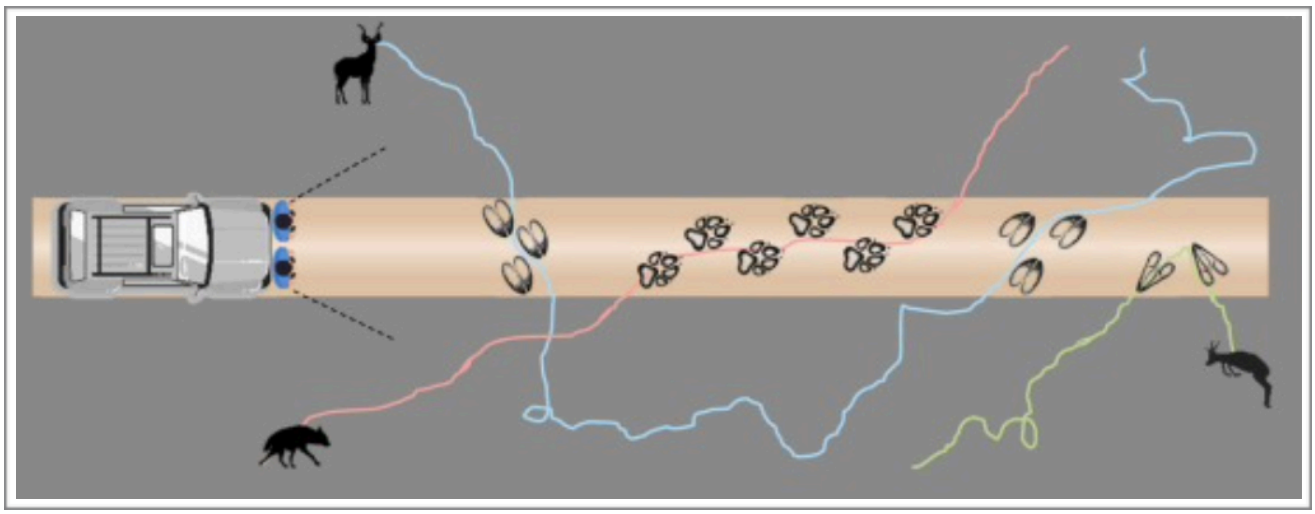

**Figure 2 : Representation of a driven track survey (the space bounded by the car wheels in sand color = transect, blue line = greater kudu path over 24 hours, red line = brown hyena path over 24 hours, green line = springbok path over 24 hours) (From Gielen et al. (2024)).**

To collect data for the FMP formula, the "track count along transects" method, presented above, must comply with a specific protocol to meet the model's assumptions. First, transect locations must be independent of animal movements, so that animals are neither attracted or repelled by the transect. Second, while an animal's trail remains on the transect, the observers will count this individual only once. If the animal leaves the transect and returns to the transect further on, it will be counted as a second track interception (Figure 2). Hence, we do not care about identifying individuals but care about how much track interceptions we see on the transect. Indeed, as the model is defined by random line encounters identifying animals will make it not random anymore.

With such protocol, the number of track interceptions collected might give the impression that the population density is greater than it really is because we sometimes have counted one individual as if there were several. By using a correction, such as the FMP formula, we take into account the average daily travel distance of the species, which will correct the overestimation (or the underestimation if DTD is less than one, such as, for small species) of the number of individuals.

Therefore, the main limitation of this formula is to use accurate and precise estimates of average daily travel distances for a given study area and study period (Keeping, 2014).

## 4) The daily travel distance

It is important to know that an individual of one species may not intercept the transects as often as an individual of another species, as this will depend on the distance each species travels over 24 hours. Some species will walk an average of 10 km in a day, and therefore, for a given sampling effort, have more chance to intercept the transects than a species that only covers an average of 3 km a day. If we do not take into account the daily distance covered by each species, we might think that each track interception by the transect belongs to different individuals, when in fact it might be a single animal.

Beside ensuring correct detection and identification of tracks, the key to obtaining accurate population density estimates ($\widehat{D}$) is to have an accurate parameter $\hat{M}$. The best way to obtain an accurate $\hat{M}$ parameter is to have empirical estimates from the study area itself.

Empirical estimates of average DTD are only available for a few species in the Kalahari, and mainly for large carnivores (Keeping, 2014). Among large herbivores, empirical estimates are available for wildebeest and oryx (Keeping, 2014; Selebatso et al., 2018). For other herbivores, average DTD are estimated allometrically (Carbone and al., 2005). It means that average DTD estimates have been calculated from a scaling rule using the species average body mass. However, Kalahari mammals for which empirical estimates were available showed greater displacements than those predicted by the allometric relationship (Keeping, 2014). Movements are often determined by energy requirements and food distribution (Williams et al., 2021). So, because of the harsh conditions in the Kalahari, it is not surprising that Kalahari mammals have higher average DTD estimates. Hence, Keeping (2014) made available a Kalahari correction factor to precisely correct density values estimated using allometric average DTD estimates. Hence, without this correction, the population density estimate would be overestimated.

To create the correction coefficient, Keeping considered 12 different species (gemsbok, wildebeest, steenbok (*Raphicerus campestris*), brown hyena (*Hyaena brunnea*), cheetah (*Acinonyx jubatus*), leopard, lion, spotted hyena (*Crocuta crocuta*), honey badger (*Mellivora capensis*), yellow mongoose (*Cynictis penicillata*), aardvark (*Orycteropus afer*), ground pangolin (*Manis temminckii*))

in 2 different orders (Artiodactyla and Carnivora). Depending on the species, the difference between their allometric DTD estimate and their empirical DTD estimate ranges from 0.45 km to 25.22 km. These differences will be reflected on the densities to a greater or lesser extent. Although definitely valuable, alimitation of the current correction coefficient is that it is identical for all species regardless of their behaviour, diet, etc. It is therefore assumed that all densities can be corrected in the same way, whereas in reality the correction needed may vary for one species to another. So, if we want to estimate the population density of a species that does not have an empirical average DTD estimate, it is still preferable to first obtain the empirical average DTD estimate where possible.

To estimate the empirical average DTD of an animal, several methods can be used.

The use of GPS collars is one of them. Before placing the collar on an individual of the target species, the researchers must program the collar to record the animal's GPS coordinates at a certain frequency (e.g. every 15 minutes, every hour, once a day, etc.). The frequency must be adapted to the research question the researchers want to answer, while ensuring that the collar's battery and memory are sufficient to collect data across the intended study period.

Once the coordinates have been retrieved, a common way of calculating the average DTD estimate is by summing straight-line distances between each coordinate received over a 24-hours period (especially used for large predator, elephants and deers) (Murphy and al., 2019; Webb et al., 2010). This method is limiting because it inevitably underestimates the value of $\hat{M}$. And, this underestimation will increase as the frequency of fixes decrease. There is another method, more precise : the continous-time speed and distance (CTSD) (Noonan et al. (2019); Brown et al. (2023)). First of all, for this technique, we need to estimate the device’s error parameters to calibrate the measurement error. Then, model selection techniques are employed to identify the best fit continous-time movement model for the data. A simulation-based approach is then employed to sample from the distribution of trajectories conditional on the data, from which the mean speed estimate and its confidence intervals can be extracted. Using simulated data, Noonan et al. (2019) demonstrate how CTSD provides accurate, scale-insensitive estimates with reliable confidence intervals (Noonan et al. (2019)).

But GPS collar is an invasive method for animals and very costly. Indeed, to fit a collar, you have to choose the right candidate, sedate it and then fit it with the collar. This operation may cause a lot of stress to the animal, and also requires considerable financial resources, with all the qualified staff and equipment that need to be present (Jewell, 2013). Another challenge regarding average DTD

estimate study involves the need of a high transmission frequency. The higher the transmission frequency, the faster the collar battery will discharge. If other studies are in progress (home range studies, dispersal movements), this may compromise the results. What's more, if the collar's battery runs out too early, it will have to be replaced, thus causing stress to the target individual again.

A promising solution for estimating daily travel distances is long-follow trailing (technique explained in section II. Materials and methods). It is non-invasive, less expensive compared with the previous method, and can be used on animals of all sizes as long as their footprints are visible on the ground and animals can be spotted. An interesting fact is that a major limitation of this method, i.e. the lack of trailing skills, is not a problem in the Kalahari, thanks to the reknown expertise of local trackers. In addition, this technique allows local communities to be involved in species conservation, providing them with an income and retaining their skills (Keeping et al., 2018).

## 5) Objectives of the study

Overall, my thesis aims to fill some gaps related to the quality of average DTD estimates for Kalahari mammals, and therefore the quality of their density estimates calculated through the FMP approach. I focus here on key Kalahari species in terms of their importance in the ecosystem and tourism industry, as well as vulnerability level to disturbance. Amongst them, five species still lack empirical data in terms of daily travel distance :

- The eland (*Taurotragus oryx*), classified as Least Concern by the IUCN Red List, is the largest antelope on the African continent. It lives in the savannahs of East and Southern Africa, but can also be found in arid areas such as the Kalahari, where there is the biggest population (The IUCN Red List of Threatened Species). The allometric estimate of the average daily distance travelled by this animal is 4.64 km (Keeping, 2014).

- The greater kudu (*Tragelaphus strepsiceros*), classified as a species of minor concern, is a woodland antelope found in Central, East and Southern Africa (The IUCN Red List of Threatened Species). The allometric estimate of the average daily distance travelled by this species is 3.6 km (Keeping, 2014).

- The red hartebeest (*Alcelaphus buselaphus*), also classified as a species of minor concern but in decline, is an antelope that lives in open savannah areas in Sub-Saharan Africa and South Africa (The IUCN Red List of Threatened Species). The allometric estimate of its average daily distance travelled is 3.36 km (Keeping, 2014).

- The springbok (*Antidorcas marsupialis*), classified as a species of minor concern but in decline in the Kalahari (DWNP, 2018), is an antelope that lives in South and West Africa (The IUCN Red List of Threatened Species). The allometric estimate of the average daily distance travelled by this animal is 2.31 km (Keeping, 2014).

- The ostrich (*Struthio camelus*), another declining species classified as being of minor concern, is the largest bird in the world, living in open areas of Africa (The IUCN Red List of Threatened Species). The allometric estimate of its average daily distance travelled is 3.05 km (Keeping, 2014).

Therefore, a first objective of this study is to obtain empirical estimates of average daily travel distances for the five species mentioned above. To meet the first objective, we spent three months trailing individuals or groups of these species in the field in Khutse Game Reserve, Botswana.

The second objective is to assess if some of the animal demographic attributes (i.e. group size, sex and social structure) and temporal parameters (progression in the season) have an impact on DTD.
My hypotheses were that all four parameters, independently, would have an impact on the DTDs. I expected that as the size of the group increased, so would the average DTD estimate, that males would have a greater DTD than females, and that groups with juveniles would have a smaller DTD than groups made up entirely of adults. Finally, I thought that the later into the dry season we went, the more the DTDs would decrease. Answering these hypotheses would give us an idea of the final impact on population density $\widehat{D}$ and therefore whether different "average DTD estimates" for the same species should be used depending on the environmental conditions taken into account (e.g. whether there is a big difference between the average DTD estimate in the rainy season and that in the dry season).

A final objective is to compare the estimates of empirical and allometric average DTD ($\hat{M}$) and to propose a correction factor for allometric average DTD estimates of Kalahari species thanks to the new data obtained.

In 2014, Keeping created a correction coefficient to be applied to population densities calculated using allometric average DTD estimates. However, we have chosen not to improve Keeping's correction coefficient itself, but to create a correction coefficient that can be applied directly to allometric average DTD estimates. With the empirical average DTD estimates of our five species added to the existing dataset of Keeping (2014), we might also potentially obtain a more accurate coefficient. Furthermore, as we now have more data for the Artiodactyla order (i.e. antelopes), we can explore the possibility to create a correction coefficient for the Artiodactyla order and another one for the Carnivora order separately.

# II. Materials and methods

## 1) Study area

The African continent is made up of an impressive diversity of ecosystems, ranging from lush tropical forests (e.g. Democratic Republic of Congo) to the most arid of deserts (e.g. Algeria and Libya), not forgetting the great savannah plains. Some African countries are dominated by one major type of ecosystem. Other countries, on the other hand, host a greater diversity of ecosystems. Tanzania, for example, encompasses savannahs (e.g. the Serengeti), forests (e.g. the Arusha Reserve) and deserts (e.g. the Lake Natron Reserve). Similarly, Botswana mainly comprises two distinct ecosystems, that is the Okavango Delta (i.e. large variety of aquatic, wetland and terrestrial habitats (Ramberg and al., 2006)) and the Kalahari Desert. The latter is part of a larger geological feature called the Kalahari Basin, which it is often confused with. The Kalahari basin covers Botswana, Namibia, South Africa, southern of Angola and Zambia and western part of Zimbabwe (Haddon et al., 2005). On the other hand, the Kalahari Desert is located at the center of Kalahari basin, and covers Botswana (the largest portion), Namibia and South Africa (David et al., 1991).
For my master’s thesis, I focus on the Kalahari Desert (referred elsewhere in the document as « Kalahari »), a huge sand-covered plain, although almost entirely vegetated.

Within the Kalahari Desert, there are several types of habitats.

The first habitat we can mention is the pan ecosystem. The pans are depressions of varying size, sub-circular or sub-elliptical in shape, with hard silty clay soils that can hold small quantities of water after a rainfall. They may be covered in grass or have bare soil. This landscape feature plays a very important role as it is a source of water after rainfall, of nutrient-rich vegetation and a source of mineral salts, too (Grove, 1969; Lancaster, 1978). The pans were formed by wind action on surfaces made bare by seasonal water accumulations (Lancaster, 1978).
Another habitat we can find in this environment is the grassland in the sandveld. This ecosystem is characterized by vegetation (mainly grass) that develops on dry and sandy soil.
We can also find "shrublands". These areas are characterized by the presence of shrubs and woody bushes (such as acacias) that generally grow in semi-arid to arid environments.
There are also "Savanna", characterized by woody plant biomass (Scholes, 2002).
We can also take into account "Dune fields", i.e. sand dunes that can be stabilized by vegetation (grasses or shrubs) or shifting (Van Rooyen and Van Rooyen, 1998).

The region experiences two main seasons : the wet season from November to April (summer with high temperatures and rainfall) and the dry season from May to October (winter with cold nights and infrequent rains). Another important feature of the Kalahari climate is the variation in temperature within 24 hours, with a difference between night and day-light hours between 15 and 20°C on average.

In particular, my study focus here on the Botswana part of the Kalahari Desert and more particularly on the south-east, in the Khutse Game Reserve (Figure 3).
Khutse G.R. is located just south of the Central Kalahari Game Reserve. It represents 2500 squares kilometers of semi-arid savannah. It was, officially, declared as a protected area in 1971 and was the second game reserve established on tribal land in Botswana (Botswana tourism, 2021).
Khutse Game Reserve grows vegetation made up of grasses (e.g. *Schmidtia pappophoroides*, *Stipagrostis uniplumis*, *Heliotropium lineare*, *Enneapogon desvauxii*...), shrubs (e.g. *Catophractes alexandri*, *Stipagrostis uniplumis*...) and trees (e.g. *Vachellia spp.* and *Senegalia spp.*) (Lori and al. 2019) creating a, more or less, open environment depending on the location.
The local fauna is diverse, including many large animal species such as lions, leopards, cheetahs, hyenas, wild dogs, wildebeests, gemsboks, elands, greater kudus, red hartebeests, elephants, giraffes, ostriches, and springboks.

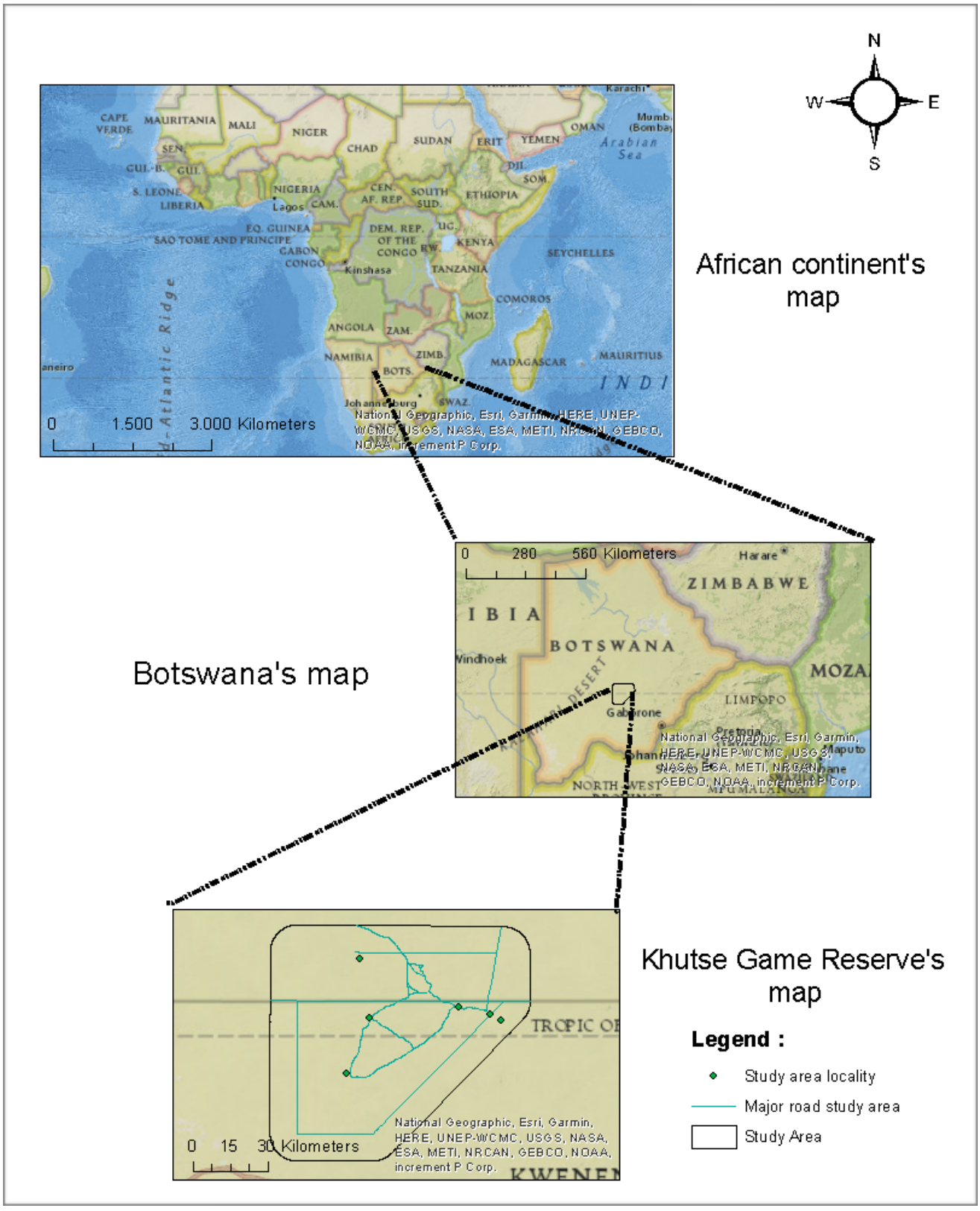


**Figure 3 : Overview of the study area within Botswana and the African continent**

## 2) Leopard Ecology & Conservation

This study has been carried out in collaboration with the non-governmental organisation named Leopard Ecology & Conservation (LEC).

Initiated by Monika Schiess-Meier in 2000, the aim of LEC is to preserve Botswana's leopard and lion populations through focused scientific research, education, and the provision of conservation management advice (Leopard Ecology & Conservation, 2023).

Two key research projects are (1) the study of population density of lions and leopards and (2) the study of lion and leopard's prey population trends in Khutse Game Reserve.

As part of the fulfilment of these objectives, LEC has recently started to apply the FMP analytical approach to their long-term track surveys in order to estimate population densities of lions, leopards, other carnivores as well as their preys within Khutse Game Reserve and surrounding communal grazing areas. Improving the estimation of large herbivores empirical average DTD, would therefore benefit the second objective of this organisation related to the prey population estimates.

This collaboration gave us access to established infrastructures and logistics, and to a place where animals can be found easily comparing to unprotected areas in the Kalahari. The most valuable contribution was the opportunity to collaborate with local certified trackers holding an immense knowledge of the study area and who were actively involved in designing the study protocols.

## 3) Field team

As part of data collection, we needed to follow the tracks of a target individual or group of individuals to record their daily travel distance. For this, the skills of Indigenous trackers come to the rescue. The Indigenous trackers belonging to the San community are the direct descendants of the oldest human lineage in the Kalahari Desert (Silberbauer, 1965; Tanaka, 1974). Some of them can read animal tracks in the sand (an ideal substrate for printing and detecting tracks) in the same

way as we are able to read a book (Liebenberg, 1990b). Their tracking skills are astonishing, enabling them to interpret the tracks and thus give us the path taken by the target individual or group of individuals. They can also give us information on the animal's sex and age class, the time of day when it passed a particular spot and the behaviour it adopted (walking, running, eating, resting, etc.).

Trackers are therefore essential team members for trailing animal paths. We also designed the data collection protocol with their help. This is an example how track-related survey methodologies make it possible to involve local populations in nature conservation (as an employment and as a collaboration), and also to preserve this precious knowledge.

Our field team consisted of two recorders interchangeably collecting data (mostly myself and LEC intern Seitshiro Pule), one driver with one car who were following us during the trailing and three trackers (Duela Seganaphofu, Senxwai Mosololo and Xee Fire Seganaphohu) that have been certified by CyberTracker Conservation's Tracker Certification System (https://cybertracker.org/tracking/tracker-certification/).

Fire and Senxwai are certified « Cybertracker secondary certificate - Track & Sign Level 3 » et « Cybertracker secondary certificate - Trailing Professional ». That is, they achieved an accuracy of ≥ 90% in track and sign identification and 100% in trailing abilities. As for Duela, he is certified « Cybertracker secondary certificate - Track & Sign Level 3 » et « Cybertracker secondary certificate - Trailing Level 3 ». I.e. an accuracy greater than or equal to 90% in track and sign identification and in trailing abilities.

## 4) Data collection

Data collection of DTDs was done through long-follow trailing of individuals of each species between the 15th May and 15th August 2023. The method involves visually spotting an individual animal or a group of individuals on day 1 at a time when animals move less and rest, typically towards the middle of the day when temperatures are higher (Owen-Smith and al., 2014; Berry, P.E. et al., 2023) (Figure 4). While keeping animal disturbance to a minimum, the following data were recorded using a customized CyberTracker (https://cybertracker.org/) application on smartphone: observers, recorder, date and time of observation, GPS location, species, number of individuals, sex, age class, behaviour (see appendix 1 for more details; behavioral data were recorded as part of a future study but will not be used for this one) and a photograph. Such information was collected to facilitate individual identification on day 2, and to better identify the exact point where to start trailing.

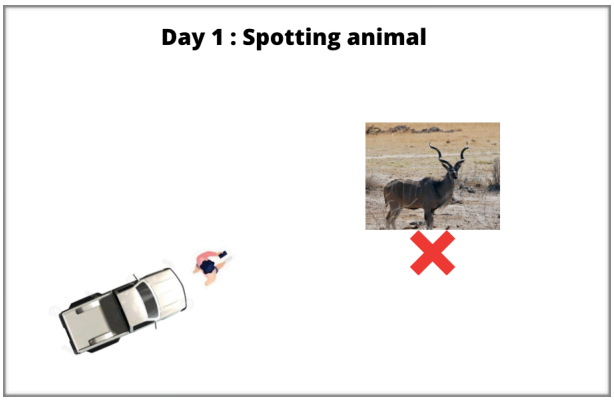


**Figure 4 : Schematic example of a spotting of a greater kudu**

Photo credit : Marie Jardeaux
Human icon source : https://www.istockphoto.com/fr/vectoriel/vue-supérieure-des-personnes-fixées-disolement-sur-un-fond-blanc-hommes-et-gm1186166480-334578180
Car icon source : https://fr.123rf.com/photo_50351195_pick-up-vue-de-dessus-isolé-sur-blanc.html

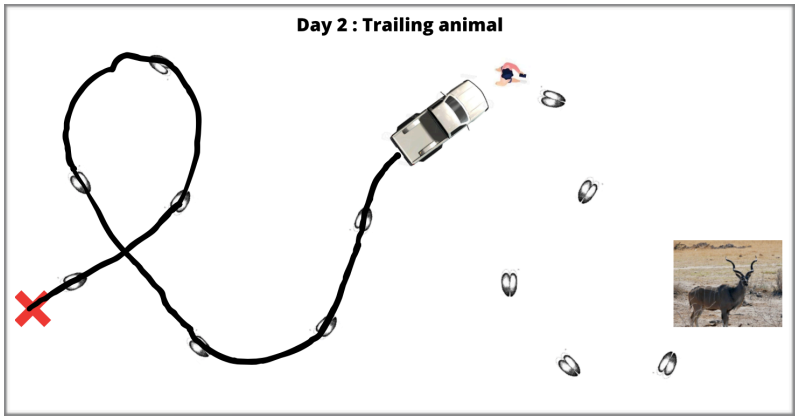


**Figure 5 : Schematic example of a trailing of a greater kudu**

Photo credit : Marie Jardeaux
Animal tracks retrieved from Liebenberg (1990)
Human icon source : https://www.istockphoto.com/fr/vectoriel/vue-supérieure-des-personnes-fixées-disolement-sur-un-fond-blanc-hommes-et-gm1186166480-334578180
Car icon source : https://fr.123rf.com/photo_50351195_pick-up-vue-de-dessus-isolé-sur-blanc.html

On day 2, the team returned to the same location approximately a minimum of 4 hours before the time the animal was spotted on day 1. From this point, the field team followed the animal's trail, until catching up with it at about the time it was spotted on day 1 (Figure 5). During the trailing, the team split up so that the trackers led the walk to find and indicate the trail. A

recorder followed them to record the exact animal path and all the information given (e.g. the behaviours, or if there was a change in the composition of the group) on the CyberTracker application. Finally, the car followed the recorder from a distance to minimize noise disturbance. The second recorder stayed on the roof of the vehicle to check for animals. Having one of the team member on the roof allowed us to be more vigilant about the proximity of the individual or the group of individuals being tracked, to record a possible spotting for the following day or to detect a possible danger (E.g. when fresh lion tracks were on the trail we were following, we could climb back in to avoid any incidents, etc.).

When the trackers could easily follow the trail, the recorder activated the trail recording by pressing the « Start » button on the application before starting walking on the trail. When the trail was difficult to see and the trackers had to look for it, the recorder indicated the trailing was paused using the « Stop » button on the application. The recorder then waited by the last point where the trail was visible. Once the trackers recovered the trail, the « Start » button was used again to indicate the trailing was resumed and the recorder started walking on the trail again. Each behaviour carried out by the animal or group and interpreted by the trackers was recorded on the application during the trailing session.

The CyberTracker application recorded one GPS fix every 1 second while walking exactly on the animal trail. Hence, we obtained a high-resolution trail and therefore could calculate a very accurate estimate of the distance covered over 24 hours by the target animal. A handheld Garmin GPSMAP64s was carried by the same recorder and the tracking function was activated to provide a back-up, in case the CyberTracker application encountered any problem in the field. However, even with the « Most Often » setting of the tracking function, the trail recorded by the Garmin GPSMAP64s was less precise than the trail recorded via CyberTracker.

In case the animal was not observed at the targeted time (i.e. 24 hours from the spotting time on day 1), the trackers continued trailing till they estimated the age of the trail corresponded to the time the animal was spotted the day before.

For our study, all spottings were carried out opportunistically along the reserve’s roads. The aim was to spot different individuals/groups of the same or different species over the course of a day, allowing us to choose which spotting would be best to use for trailing the following day. This

choice depended on the spatial and temporal distribution of data already collected, and on the scarcity or elusiveness of the species spotted. We also paid attention to the time when the spotting was done to ensure enough time to complete the trailing the following day, which starts from dawn at the earliest. Choosing a spotting time of around midday also gave us a better chance of finding the animals we were trailing resting. As a result, we were allowed a margin of error if we found them too early or too late. Finally, we also minded the place where we had spotted the species, in particular if it was a pan because we knew that the trailing was going to be more complicated because of the hard soil, which characterizes this environment, on which the footprints are badly imprinted.

Appendices 1 and 2 detail the CyberTracker application used to collect data and the field protocol respectively.

## 5) Data treatment

Once the long-follow trailing was completed, the data from the CyberTracker application and the Garmin GPS MAP64s were uploaded, respectively, onto CyberTracker and Basecamp software, to extract the path travelled by the target animal in 24h.

The path obtained then was cleaned of unnecessary points. In this regard, the « Start/Stop » system of our CyberTracker application, allowed us to indicate a pause in the trailing when the trackers temporarily search for the trail or a break was needed. Using ArcGIS 10.8.0, any erratic GPS fix point before a Start or after a Stop (i.e. when the recorder was still immobile before finishing entering a stop on the phone or after pressing start to resume the trail) were removed, to obtain the most accurate daily distance travelled by the animal.

A common technique used in movement data curation involve « smoothing » paths using specific algorithms, for example, to round off certain angles in the trails that may be due to GPS accuracy error. However, we chose not to use this technique. In fact, the precision of Smartphone's GPS and trackers' expertise enabled us to obtain the precise path taken by the individual or group. In addition, given the density of vegetation, the animals might sometimes need to go around bushes, and with smoothing this slight detour would probably have been eliminated. Another reason for not using this tool is that certain species, such as ostriches in our case, have a particular way of moving in zig zags while foraging, which could have been altered if we had smoothed their trails. This would therefore have distorted the results obtained for the average DTD estimates.

The clean trails were then classified as « unbiased » or « biased ». A trailing was defined as « unbiased », when all the following criteria were met : (1) the trailing covered the required 24 hours, (2) the animals we followed did not see, smell or hear us, and consequently did not run because of us, (3) at the end of the trailing and therefore at the required time, the followed animals were seen or the team found the place where they were resting or foraging just before they ran away because of us. In some rare cases, the animals were found resting in a place within the 25th hour. When trackers confidently estimated that they have been resting at that place already when the 24h were completed, the trailing was considered « unbiased ». Trailings that didn't meet one of these three criteria were considered as potentially « biased ».
Among the potentially biased trails, sources of error therefore needed to be identified and corrected if possible.

During some trailings, we failed to see the target animal at the end or to find the place where it was resting/foraging at the targeted time. In these cases, the trackers carried on trailing and had to estimate the age of the trail ; the trailing was ended when trackers estimated the 24 hours trail to be completed. When the trail was very fresh, less than 2 hours old, we can reasonably believe the trackers to be quite accurate in their estimation (Liebenberg, 1990). Over 2 hours old, the sources of error risks to become too great due to the multiplication of environmental factors potentially affecting the preservation of animal tracks on the ground.

In some cases, we didn't manage to complete the 24 hours. There were several reasons for that such as the trail was difficult to follow because of the soil characteristics (e.g. the hard substrate of pans), or the animals walked a lot because of predators, the wind, etc. If a minimum of 22 hours of the trail was already completed, we believe we can reasonably estimate the distance covered by the animals during the last 2 hours based on the distance covered during the 22 hours period.
The error is likely to be smaller or equal to the one associated to estimation of the age of the trail (see previous point), but anyway smaller than the one associated with the choice of our sample (i.e. individuals/groups we trailed). However, if less than 22 hours of the trail was completed, the sources of error are likely too great for reliably estimating the distance covered during the missing hours where the behaviour of the animals are unknown.

Another source of error arises when the observers, unwillingly, caused the animals to run away from them. This behaviour can happen at the beginning of the trail due to the spotting, or during the trailing when observers caught up with the animals before the 24h has elapsed. The distance covered during these observer-induced running portions can potentially significantly increase the DTD value of the trail. We however decided to make an exception for the greater kudus. Indeed, these animals were very fearful and fled at the slightest noise. Therefore, when they ran less than 100 meters across the entire trailing, we decided to define it as « Unbiased ».

The potentially biased trails, resulting from the presence of one or several of these errors, needed to be further examined for consideration in our final dataset. As our original sample size is limited, each trail we exclude from the dataset would have a significant cost in terms of analytical power and precision in the calculation of the final average DTD estimates. Excluding trails must be therefore done only if there are statistical or contextual reasons indicating a specific trail is clearly an outlier or unreasonable to use.
In this study, we used the unbiased trails to determine if a potentially biased trail is an outlier according to descriptive statistics.

First, a DTD mean and a standard deviation (SD) were calculated out of the unbiased trails for each species.
Second, we kept and corrected the trails considered as potentially biased as follows :

- The completed 24h trails for which the trackers had to estimate the end of it were kept unless the estimation was done 2 hours past the spotting time.
- For trails containing running portions induced by us, we removed these parts as the race only covered a few minutes over the 24 hours, and leaving them could substantially biased the DTD towards the higher end.
- Incomplete trails (i.e. < 24h) were extrapolated if the trail already covered 22 hours and was past 10am in the morning as animals where often observed to rest for a significant amount of time during the night and being most active in the early morning.

Finally, after correction, the potentially biased trails whose DTD values fell within 2 times the SD (i.e. within a 95% confidence interval) of the unbiased trails were considered as unbiased, and included in the final dataset. When falling outside 2 times the SD of the unbiased trails, they were considered biased and excluded from the final dataset.

## 6) Variables tested for their impact on the DTD

As part of the study, we wanted to know whether certain environmental or demographic variables could have an impact on DTD estimates.

Thinking about how to avoid as much bias as possible for our study, we thought about some characteristics that could influence the average of our DTD.

While recording our trailings, we used the CyberTracker application, which we collected several parameters with such as the size of the group. Can the group size influence the DTD of our species ? Our hypothesis is that larger is the group, the individuals will have to walk more to find the resources needed for their survival (Markham et al., 2015; Wang et al., 2021).

The group size variable was included in the design of the data collection in CyberTracker but the question « how to use this information to assess its impact » was defined at the end of the field period.

It was, initially, a continuous variable of actual group size numbers. For the analysis, we still use it as a continuous variable (Table 1), although we have assigned a rank to each group size number and distance traveled. This allowed us to test our hypothesis more effectively (see 7) Data analysis).

We also recorded the sex composition of the group in the CyberTracker application. Do the sex of individuals influence the distance traveled in one day ? Our hypothesis is that males have to travel further to defend their territory and to reproduce as shown by Greenwood (1980).

The sex structure was also included in the design of the data collection in CyberTracker but, the question « how to split them in meaningful categories » was defined at the end of the field period. For the sex, we separated each trailing in function of the following categories : « male » (group with males only), « female » (group with females only) and « mixed » (group with males and females). We chose to include a "female" category to check whether there was a significant difference between males and females (without being influenced by the males in a group) (Table 1). We used these categories to test our hypothesis statistically.

The age structure of the group was recorded too with CyberTracker application to be able to determine its social structure. Do the social structure of the group influence the daily travel distance?

Our hypothesis is that groups with juveniles travel shorter distances to adapt to the physical conditions of the youngest as shown by Debeffe et al. (2019), Shimooka (2005) Inoue et al. (2016).
As for the previous variable, we have defined the meaningful categories at the end of the field period. For the social structure, we separated each trailing in function of the following categories : « adults » (no subadults or juveniles in the group) and « family » (with subadults or juveniles in the group) (Table 1). These categories were used to test our hypothesis statistically.

Another possible impact on DTD is the difference in conditions between the dry and the wet season. During the wet season, temperatures are high and precipitations are frequent while for the dry season, temperatures are cooler and there is practically no precipitation. These weather changes might have also an impact on food and water availability. So, they might have an impact on the DTD of the different species such as shown for elephants by Birkett et al. (2012).
We could not statistically test this hypothesis because we only conducted the study during the dry season. But, we wanted to know if there was an evolution of the DTD during the dry season.
Among the data we collected were the dates each trail was recorded. We were therefore able to obtain the exact number of days since the first day in the field. This allowed us to test the impact that the temporal progress in the first half of the dry season had on DTD (Table 1). According to Martin et al. (2015) and Naidoo et al. (2012), during the rainy season, animals walk more because they can move further away from watering holes and find better quality food. Based on this information, we therefore hypothesize that as the dry season progresses, the distances covered daily will become shorter.

**Table 1 : Summary of the different variables tested for their impact on DTD.**

| Variable | Type of variable | Categories |
|---|---|---|
| Group size | Continuous | X |
| Sex composition of the group | Categorical | Male / Female / Mixed |
| Age structure of the group | Categorical | Adults / Family |
| Temporal progress in the dry season | Continuous | X |

# 7) Data analysis

## a) Verification of data normality to calculate the average DTD estimate per species

In order to accurately calculate the empirical average DTD estimate per species and classical measures of data dispersion around it (variance, standard deviation, etc.), our data should follow a normal distribution. First, we tested the normality of the unbiased trailings to justify the calculation of their mean and standard deviation, and thus identify the biased trailings that fell within the interval of twice the standard deviation. Secondly, we tested the normality of our final dataset.
As we had a limited amount of data within each species, we pulled them together to increase the analysis power in testing data for normality. We applied a group-mean centering on the « species » variable by moving the « species » variable's mean DTD to zero. This was done within each category (i.e. each species) by subtracting the mean DTD of this category from each observation (i.e. trail's DTD). So all species had the same mean DTD (i.e. zero), which made observations between species comparable, and therefore they can be analyzed as one same dataset. Then, standardizing the « species » variable moves its standard deviation to one, which was done within each category by dividing the centered observations by the standard deviation of this category. This ensured homoscedasticity to avoid skewed or biased results. By applying the above standardization in our case, it means that we suppose that there are no differences in DTD between species, so the effect of this parameter does not exist anymore.

After standardizing all our dataset, we used a Shapiro-Wilk test to check if our data had a normal distribution.

## b) Effect of group size on DTD

To find out whether the group size has an effect on the DTD, we had several options.

First, we could have compared DTD means between categories of group size. Given our small sample size, the variable « group size » could be divided in two categories only, e.g. « small group size » and « large group size ». However, the group size values associated to the different trails are originally from a continuous variable. It was therefore complicated to set the limit between what to consider as a « small group size » and a « large group size ». It also came with the risk of severely unbalanced datasets between categories.

We therefore choose another option, which was to test the existence of a monotonic relationship, i.e. to study how DTD and group size evolve together but without inferring the rate of evolution (e.g. if one increases/decreases, the other does the same as a positive correlation, but not necessarily at a constant rate). To do this, we transformed the variables "DTD" and "group size" into ranks, following the idea of Spearman's correlation analysis :

- the smallest value of DTD was given the rank of 1, the second smallest was given the rank of 2, and so one.
- the smallest value of group size was given the rank of 1, the second smallest was given the rank of 2, and so one.

Ex-aequo values were given the mean rank between them, as it is important that the number of ranks corresponds to the total number of observations. For instance, if group size observations are 1; 3; 5; 5; 8; 9, their ranks will be 1; 2; 3.5; 3.5; 5; 6 where 3.5 = (3 + 4) / 2.

The monotonic relationship can then be tested through a linear regression model such as $Y = \beta_0 + \beta_1 * X_1 + \varepsilon$ on ranked variables, with :

Y = DTD's rank

$\beta_0$ = Intercept

$\beta_1$ = Scaling exponent

$X_1$ = Group's rank

$\varepsilon$ = Error term

However, the difference in mean ranked DTD between species is directly linked to the number of trails done for each species, not the trails' distance value anymore. Therefore, it makes no sense to test the species effect after applying the ranking. This is actually not a problem since we anyway have no need to test for the species effect on DTD; we know for a fact each species has its unique mean DTD value and we are not interested in their difference.

We can therefore force the species effect to be null by centering ranked DTD values and ranked group sizes within each species. That way, all species will have a ranked DTD mean and ranked group size mean of zero (i.e. $\beta_0 = 0$). We should also further standardize ranked DTD values and ranked group sizes within each species to force all groups of species to have the same variance (i.e. SD = 1) in terms of ranked DTD and ranked group size. This is desirable for meeting the homoscedasticity assumption of linear regression.

Note that we have chosen not to include the ostrich data in this analysis, due to small sample size, and given that four out of five trails had two individuals and the last trail had eight individuals. Therefore, a ranking would result in having four time the rank 2.5 and one time the rank five. So, here, the relationship between ranked group size and ranked DTD would hold in two points. So, a change in the point ranked as five in particular has the potential to have a big impact on the shape of this relationship.
Another remark, in relation to the vagaries of the field, is that when the initial group we were following split up, during a trailing session, we decided to follow the largest group formed after the split.

After standardizing all the data we needed, we fitted a linear model using the *lm* function in R (version 4.3.1), to test the effect of standardized ranked group size, as well as its interaction with the species variable, on the standardized ranked DTD. Then, we applied an ANOVA on our resulting model to assess the overall significance of the effects of the variables tested.
We checked the model assumptions using diagnostic plots generated in Rstudio. We assessed the linearity of the model, the independence of errors, the homoscedasticity, the presence of outliers and influential observations, and the normality of errors.
To illustrate the results, we created graphs showing the relation for each species.

## c) Effect of sex on DTD

The variable sex is a categorical variable, so is the variable species. Therefore, we modeled a two-ways ANOVA to test the difference of mean DTD between sex categories (male, female and mixed), species categories (springbok, eland, greater kudu, red hartebeest), and their interaction.
Ostrich was not included as a species category since it has only mixed value of sex.
To carry out an two-ways ANOVA, we had to ensure to meet the model's assumptions, though our study design and  using Rstudio. One of the assumptions to be verified is the independence of the observations. In our case, given that we have taken care to ensure that each DTD is collected out on different individuals or groups, we can consider the observations to be independent assess the homoscedasticity of errors and normality of residuals, complemented by Levene's test and Shapiro-Wilk test respectively.

## d) Effect of social structure on DTD

The variable social structure is a categorical variable, so is the variable species. Therefore, we modeled a two-ways ANOVA to test the difference of mean DTD between social structure categories (« adults », without subadults and juveniles, and « family », with subadults and juveniles), species categories (eland, red hartebeest, greater kudu, springbok and ostrich), and their interactions.

To carry out this two-ways ANOVA, we verified the model's assumptions similarly to the "Effect of sex on DTD" section.

## e) Effect of temporal progress in the dry season on DTD

In order to calculate whether the DTDs increased, decreased or remained unchanged as function of the number of days from the start of the project, we numbered the days from the first trailing we carried out to the last one.

Trail collection began on the 16/05/2023, which was therefore given the number 1, the 17/05/2023 was given the number 2, etc.

We then used a linear model testing for the effect of species on DTDs, the temporal progress in the dry season (number of days) on DTDs, and their interaction on DTDs.

We verified the same model's assumptions as for the "Effect of group size on DTD" section, using the same tests.

## f) Prediction of empiric DTD in function of allometric DTD estimates

In order to apply the FMP, the estimation of allometric average DTD is the current alternative used when the empirical estimate is not available for a given species. In 2005, Carbone et al. created different average DTD estimate-body mass scaling rules for different orders of mammals, using species from diverse ecosystems for which the empirical estimate of average DTD was known.

Keeping (2014), to apply the FMP formula, used Carbone's scaling rules to calculate allometric average DTD estimates for species without empirical average DTD estimates with their best available body mass estimates. The allometric average DTD estimates is obtained through the following equation : $\ln(\text{allometric average DTD estimate}) = \beta_0 + \beta_1 * \ln(\text{body mass})$, where $\beta_0$ and

$\beta_1$ have different values for the Artiodactyla order (respectively -0,11 and 0,26) compared to the Carnivora order (0,147 and 0,421) (Carbone et al., 2005). Thanks to this technique, we calculated the allometric average DTD estimate of our five target species. We could therefore compare them directly with empirical estimates obtained in the field.

For species belonging to the Artiodactyla and Carnivora orders, Keeping (2014) has also created a correction coefficient to be applied directly to the population densities obtained by FMP with allometric average DTD estimates.

As for us, with our results, we would like to create a correction coefficient to apply directly to allometric average DTD estimates and not to population densities. Note that Carbone et al. (2005) also created average DTD estimate-body mass scaling rules for other orders : Rodentia and Primates. We decided not to use the Primates order because we focus on the animals present in Kalahari. Apart from the baboons (*Papio ursinus*) and the vervet monkey (*Chlorocebus pygerythrus*), there are no other primates in the Kalahari on which the FMP formula can be applied. For the Rodentia, we chose not to use them because we had a limited dataset for this order.

To do so, first, we created a single regression with the interaction between allometric average DTD estimate and orders, on which we assessed if the intercept was different from zero or not. Then, we drew two linear regressions representing the empirical average DTD estimate as a function of the allometric average DTD estimate, one by order, using allometric and empirical DTD data for eight species of Artiodactyla and nine species of Carnivora (with outliers) (Table 24).

If the linear regression results show that the intercepts, for the Artiodactyla and for the Carnivora, are not significantly different from zero, that means we have two choices :

(1) to keep the intercept as different from zero so we don't force the slope $\beta_1$ but we increased the risk of overfitting.
(2) To force the intercept to be equal to zero so we also force the slope $\beta_1$ to change, but we may decrease the risk of overfitting. This would allow better generalization of the correction factor to apply to other data.

In our case, since the intercept was not significantly different from zero, forcing $\beta_0$ to zero makes more sense. Indeed, from a mathematical point of view, if the estimate allometric DTD average is equal to zero, this means that the animal has a weight equal to zero and therefore the estimate empirical DTD average is equal to zero. We therefore applied the following linear regression model : Empirical average DTD estimate = $\beta_1$ * allometric average DTD estimate.

We therefore created the linear regressions models for Artiodactyla and Carnivora separately, to build our correction coefficients for each order. We checked the model assumptions using diagnostic plots generated in Rstudio. We assessed the linearity of the model, the normality of errors and the homoscedasticity of errors.

We used the $R^2$ statistic as a measure of the quality of prediction of the output model, hence the quality of the proposed correction coefficient.

# III. Results

After 75 field days across 3 months of data collection (15th May to 15th August 2023), we collected a total of 71 trails all species combined (Table 2, see Appendice 1 for more details).

**Table 2 : Summary of the data collection**

| | Trail completed (24h) | Trail not completed (<24h) | Total number of trails |
|---|---|---|---|
| **Eland** | 12 | 2 | 14 |
| **Kudu** | 19 | 2 | 21 |
| **Hartebeest** | 13 | X | 13 |
| **Springbok** | 13 | X | 13 |
| **Ostrich** | 4 | 6 | 10 |

Among all the trails collected, some can be considered as potentially biased (see II. 5- Data treatment) and had to be corrected (see next section).

## 1) Final dataset for analysis and average DTD estimate

### a) Average DTD estimate for each species

To get the most out of our trails, we looked at all possible biases that could have occurred during them. We have defined the following categories of bias :

- « Running » : when the target animals ran because of us while we were following them (because they heard, smelled or saw us).
- « Estimation » : when we did not manage to see the animals on time but we continued trailing until the trackers estimated where the animals were at the required time.
- « Incomplete » : when we lost the trail of the animal or when we didn’t have the time to complete the trail before dark and, so, didn’t manage to complete the 24 hours of trailing

- **For the eland trails :**

First of all, we have separated the unbiased trails from the potentially biased trails. Of the 14 trailings carried out, nine can be considered « unbiased ».

So, to get the average DTD estimate and the measures of data dispersion around it of the « unbiased » data, we used nine of 14 trails (Appendix 2).

Using the necessary commands in Excel, we obtained the results presented in the Table 3.

**Table 3 : Summary of the average DTD estimate and the measures of data dispersion around it for the unbiased eland trails**

| | |
|---|---|
| **Average DTD estimate (km)** | 10.578 |
| **Variance of the average DTD estimate (km)** | 27.345 |
| **Standard deviation of the average DTD estimate (km)** | 5.229 |
| **Standard deviation multiplied by 2 (km)** | 10.458 |

Then we corrected the potentially « biased » DTD (Table 4).

Among the trails to be corrected, two were categorized as « Running ». In this case, on the ArcGIS, we measured the distance covered by the elands while they were running. We, then, subtracted this portion of the race from the trail length to obtain the final trail length.

Two trails were categorized as « Incomplete ». But, one was classified as a contextual outlier and excluded from the final dataset (without correction) and the other one was not eligible for correction because too many hours were missing.

Finally, one trail was categorized as « Estimation ». Here, we did not find a place where animals were resting or foraging, they continued to walk. So we checked if the estimation was done within two hours past the target time.

The corrected trails were then checked to determine whether their lengths fell within two times the standard deviation of the average length of the unbiased trails, so between 120m and 21.036 km.

**Table 4 : Dataset of eland trails : presentation of potential biases, correction of daily travel distance values, and inclusion in the final dataset**

| Trail length (km) | Trail quality | Biased trail category | Corrected trail length | Inclusion in the final dataset | Reason of exclusion |
|---|---|---|---|---|---|
| 10.673 | Unbiased | | 10.673 | Yes | |
| 6.113 | Unbiased | | 6.113 | Yes | |
| 19.832 | Unbiased | | 19.832 | Yes | |
| 17.188 | Unbiased | | 17.188 | Yes | |
| 18.851 | Biased | Incomplete, Estimation | NA | No | Too many fire trails, in 2 days, which are longer than average |
| 12.890 | Unbiased | | 12.890 | Yes | |
| 4.856 | Unbiased | | 4.856 | Yes | |
| 5.514 | Unbiased | | 5.514 | Yes | |
| 8.298 | Unbiased | | 8.298 | Yes | |
| 9.841 | Unbiased | | 9.841 | Yes | |
| 13.123 | Biased | Estimation | 13.123 | Yes | |
| 13.415 | Biased | Running | 12.200 | Yes | |
| 5.855 | Biased | Running | 5.086 | Yes | |
| 14.144 | Biased | Incomplete | NA | No | Too many missing hours, leading to too much uncertainty in extrapolating the trail length |

One trail was not eligible for correction. For this one, as less than 22 hours was completed, an extrapolation was too uncertain. So, in any case, no correction was applied to it.

Finally, one marked as « Incomplete, Estimation» was not included in the final dataset for another reason. It met the required criteria to be corrected, but we chose not to do so. In the middle of July, there were bush fires in the reserve. And while elands are normally shy animals that we had a hard time finding, they were coming close to the roads and waterholes (so we had more ease to spot

them). However, they would cover distances much longer than those travelled without the fires. Indeed, they need to avoid the fires and to find food. We, therefore limited the number of trails done during the fire period to two to limit the risks of overestimating the average DTD.

At the end, with all the trailings we kept (12), we calculated the final DTD estimate average, the standard deviation, the standard error and the 95% confidence interval (Table 5).

**Table 5 : Summary of the average DTD estimate and the measures of data dispersion around it for the elands trails included in the final dataset**

| | |
|---|---|
| **Allometric DTD estimate (km)** | 4.64 |
| **Final empirical average DTD estimate (km)** | **10.468** |
| **Standard deviation of the empirical average DTD estimate (km)** | 4.842 |
| **Standard error of the empirical average DTD estimate (km)** | 1.398 |
| **95% Confidence interval around the empirical average DTD estimate** | 3.076 |

The difference between the allometric (4.64 km) and empirical (10.468 km) estimates of the average DTD is substantial. Indeed, the empirical estimate is 2.26 times greater than the allometric estimate.

A map of the various eland trails retained in the final dataset has been produced (Figure 6) to give a better idea of their distribution in Khutse Game Reserve.

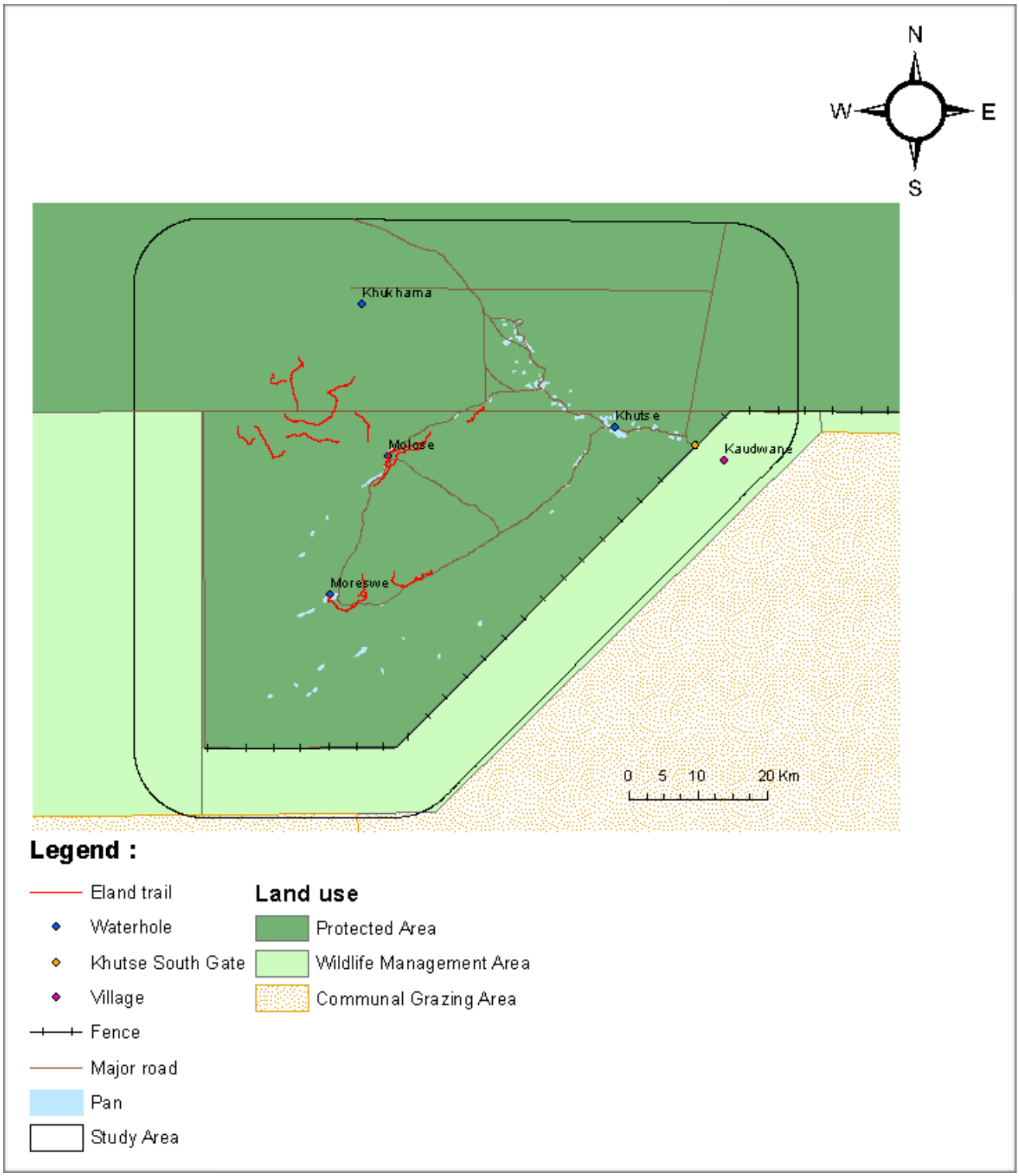


**Figure 6 : Distribution of the 12 Eland trails collected in Khutse Game Reserve, Kalahari, Botswana, and used for the analysis**

- **For the red hartebeest trails :**

Of the 13 trailings carried out, seven can be considered « unbiased ».

So, to calculate the average DTD estimate and the measures of data dispersion around it for the unbiased trails, we used seven of 13 trails (Appendix 3).

Using the necessary commands in Excel, we obtained the results presented in the Table 6.

**Table 6 : Summary of the average DTD estimate and the measures of data dispersion around it for the unbiased red hartebeest trails**

| | |
|---|---|
| **Average DTD estimate (km)** | 5.350 |
| **Variance of the average DTD estimate (km)** | 13.817 |
| **Standard deviation of the average DTD estimate (km)** | 3.717 |
| **Standard deviation multiplied by 2 (km)** | 7.434 |

Then we corrected the « biased » DTD.

We identified six biased trails, amongst which five « running » and two « estimation » trails (one trail is « Running, Estimation »). Six trails were corrected and checked against the interval of two times the standard deviation around the unbiased trails' average DTD estimate.

And, using the results obtained in the Tables 6 and 7, we finalized our dataset to calculate the final average DTD estimate for this species.

**Table 7 : Dataset of red hartebeest trails : presentation of potential biases, correction of daily travel distance values, and inclusion in the final dataset**

| Trail length (km) | Trail quality | Biased trail category | Corrected trail length (km) | Inclusion in final dataset |
|---|---|---|---|---|
| 3.217 | Unbiased | | 3.217 | Yes |
| 5.977 | Biased | Running, Estimation | 5.790 | Yes |
| 10.466 | Biased | Estimation | 10.466 | Yes |
| 11.162 | Unbiased | | 11.162 | Yes |
| 10.261 | Biased | Running | 9.162 | Yes |

| | | | | |
|---|---|---|---|---|
| 6.266 | Unbiased | | 6.266 | Yes |
| 1.881 | Unbiased | | 1.881 | Yes |
| 9.026 | Unbiased | | 9.026 | Yes |
| 4.774 | Unbiased | | 4.774 | Yes |
| 4.646 | Biased | Running | 4.253 | Yes |
| 3.040 | Biased | Running | 2.933 | Yes |
| 1.124 | Unbiased | | 1.124 | Yes |
| 6.166 | Biased | Running | 5.904 | Yes |

After applying all the necessary corrections, all the trails were retained.

So at the end, with all the trailings we kept (13) (Table 7), we calculated the final DTD estimate average, the standard deviation, the standard error and the 95% confidence interval (Table 8).

**Table 8 : Summary of the average DTD estimate and the measures of data dispersion around it for the red hartebeests**

| | |
|---|---|
| **Allometric DTD estimate (km)** | 3.36 |
| **Final empirical average DTD estimate (km)** | **5.843** |
| **Standard deviation of the empirical average DTD estimate (km)** | 3.266 |
| **Standard error of the empirical average DTD estimate (km)** | 0.906 |
| **95% Confidence interval around the empirical average DTD estimate** | 1.974 |

The difference between the allometric (3.36 km) and empirical (5.843 km) estimates of the average DTD is substantial. Indeed, the empirical estimate is 1.74 time greater than the allometric estimate.

A map of the various red hartebeest trails retained in the final dataset has been produced (Figure 7) to give a better idea of their distribution in Khutse Game Reserve.

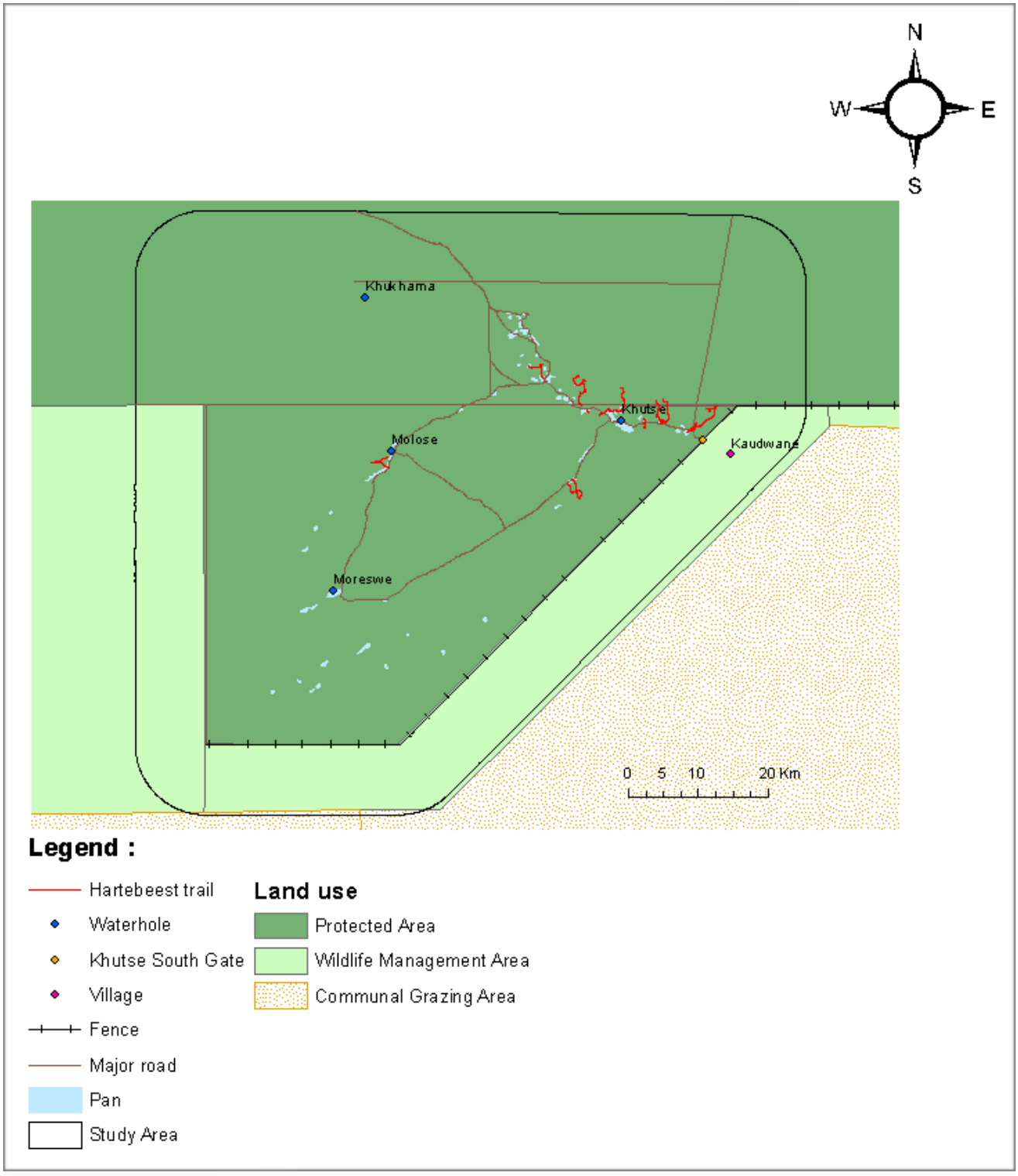


**Figure 7 : Distribution of the 13 Red Hartebeest trails collected in Khutse Game Reserve, Kalahari, Botswana, and used for the analysis**

- **For the greater kudu trails :**

Of the 21 trailings carried out, nine can be considered « unbiased ».

So, to get an initial idea of the average DTD estimate and the measures of data dispersion around it, we used nine of 21 trails (Appendix 4).

Using the necessary commands in Excel, we obtained the results presented in the Table 9.

**Table 9 : Summary of the average DTD estimate and the measures of data dispersion around it for the unbiased greater kudu trails**

| | |
|---|---|
| **Average DTD estimate (km)** | 6.680 |
| **Variance of the average DTD estimate (km)** | 7.036 |
| **Standard deviation of the average DTD estimate (km)** | 2.653 |
| **Standard deviation multiplied by 2 (km)** | 5.305 |

Then we corrected the « biased » DTD.

We identified 12 biased trails, amongst which eight « running », four « estimation » and two « incomplete » trails (two trails are « Incomplete, Estimation »). The eight « running » trails were corrected. Together with the one « estimation » trail, they were checked against the interval of two times the standard deviation around the unbiased trails' average DTD estimate. Three trails were discarded; two « incomplete » ones because too many hours were missing and one « running » one because the DTD value fell outside of the interval of the two times the standard deviation.

And, using the results obtained in the Tables 9 and 10, we finalized our dataset to calculate the final average DTD estimate for this species.

**Table 10 : Dataset of greater kudu trails : presentation of potential biases, correction of daily travel distance values, and inclusion in the final dataset**

| Trail length (km) | Trail quality | Biased trail category | Corrected trail length (km) | Inclusion in final dataset | Reason of exclusion |
|---|---|---|---|---|---|
| 7.171 | Unbiased | | 7.171 | Yes | |
| 3.566 | Biased | Estimation | 3.566 | Yes | |

| | | | | | |
|---|---|---|---|---|---|
| 1.299 | Biased | Incomplete, Estimation | NA | No | Too many missing hours, too much uncertainty in the trail age estimation |
| 0.299 | Biased | Incomplete, Estimation | NA | No | Too many missing hours, too much uncertainty in the trail age estimation |
| 4.390 | Biased | Running | 4.255 | Yes | |
| 6.867 | Biased | Running | 6.510 | Yes | |
| 8.177 | Biased | Estimation | 8.177 | Yes | |
| 6.639 | Unbiased | | 6.586 | Yes | |
| 4.815 | Biased | Running | 3.773 | Yes | |
| 5.780 | Unbiased | | 5.780 | Yes | |
| 2.815 | Unbiased | | 2.752 | Yes | |
| 1.504 | Biased | Running | 1.329 | No | DTD value falls outside SD*2 of unbiased trails |
| 11.168 | Unbiased | | 11.168 | Yes | |
| 6.911 | Biased | Running | 6.774 | Yes | |
| 5.581 | Biased | Running | 5.354 | Yes | |
| 8.951 | Unbiased | | 8.951 | Yes | |
| 3.040 | Unbiased | | 2.995 | Yes | |
| 7.364 | Unbiased | | 7.296 | Yes | |
| 3.407 | Biased | Running | 3.105 | Yes | |
| 7.419 | Unbiased | | 7.419 | Yes | |
| 3.720 | Biased | Running | 3.522 | Yes | |

At the end, with all the trailings we kept (18) (Table 10), we calculated the final DTD estimate average, the standard deviation, the standard error and the 95% confidence interval (Table 11).

**Table 11 : Summary of the average DTD estimate and the measures of data dispersion around it for the greater kudus**

| | |
|---|---|
| **Allometric DTD estimate (km)** | 3.6 |
| **Final empirical average DTD estimate (km)** | **5.842** |
| **Standard deviation of the empirical average DTD estimate (km)** | 2.357 |
| **Standard error of the empirical average DTD estimate (km)** | 0.711 |
| **95% Confidence interval around the empirical average DTD estimate** | 1.172 |

The difference between the allometric (3.6 km) and empirical (5.842 km) estimates of the average DTD is substantial. Indeed, the empirical estimate is 1.62 time greater than the allometric estimate.

A map of the various greater kudu trails retained in the final dataset has been produced (Figure 8) to give a better idea of their distribution in Khutse Game Reserve.

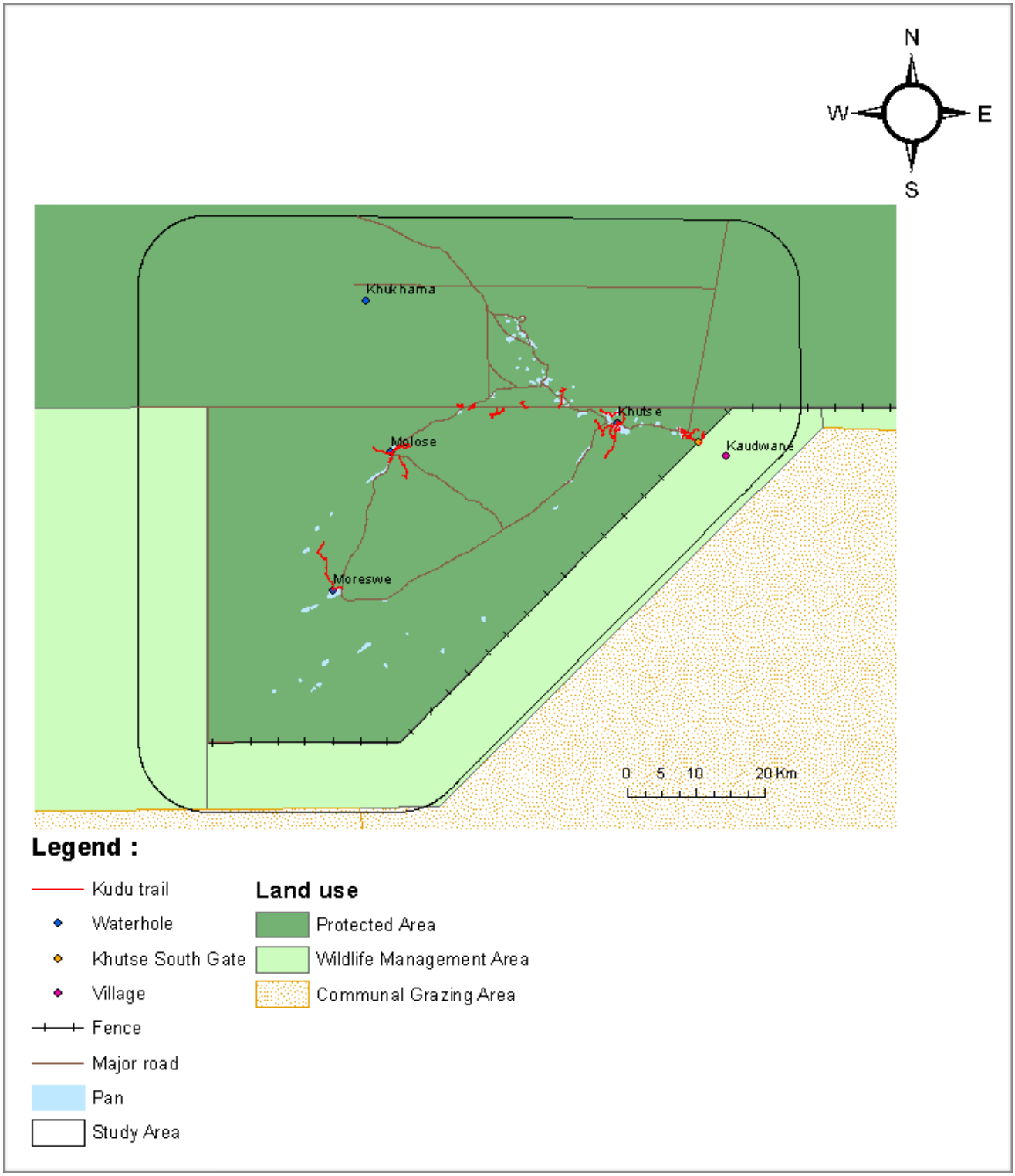


**Figure 8 : Distribution of the 18 Greater Kudu trails collected in Khutse Game Reserve, Kalahari, Botswana, and used for the analysis**

- **For the springbok trails :**

For this species, all the trails were unbiased so there was no need for corrections.

**Table 12 : Classification of springbok trails**

| Final trail length (km) | Inclusion in final dataset |
|---|---|
| 2.411 | Yes |
| 1.591 | Yes |
| 2.903 | Yes |
| 2.306 | Yes |
| 2.023 | Yes |
| 1.145 | Yes |
| 1.812 | Yes |
| 1.654 | Yes |
| 1.704 | Yes |
| 0.899 | Yes |
| 1.256 | Yes |
| 1.611 | Yes |
| 1.962 | Yes |

With all the trailings we kept (13) (Table 12), we calculated the final DTD estimate average, the standard deviation, the standard error and the 95% confidence interval (Table 13).

**Table 13 : Summary of the average DTD and the measures of data dispersion around it for the springboks**

| | |
|---|---|
| **Allometric DTD estimate (km)** | 2.31 |
| **Final empirical average DTD estimate (km)** | **1.790** |
| **Standard deviation of the empirical average DTD estimate (km)** | 0.545 |
| **Standard error of the empirical average DTD estimate (km)** | 0.151 |

| | |
|---|---|
| **95% Confidence interval around the empirical average DTD estimate** | 0.296 |

Unlike the other species studied, springboks are the only ones to have an empirical average DTD estimate lower than its allometric average DTD estimate. Indeed, the empirical estimate (1.79 km) is 0.775 time smaller than the allometric estimate (2.31 km).

A map of the various springbok trails retained in the final dataset has been produced (Figure 9) to give a better idea of their distribution in Khutse Game Reserve.

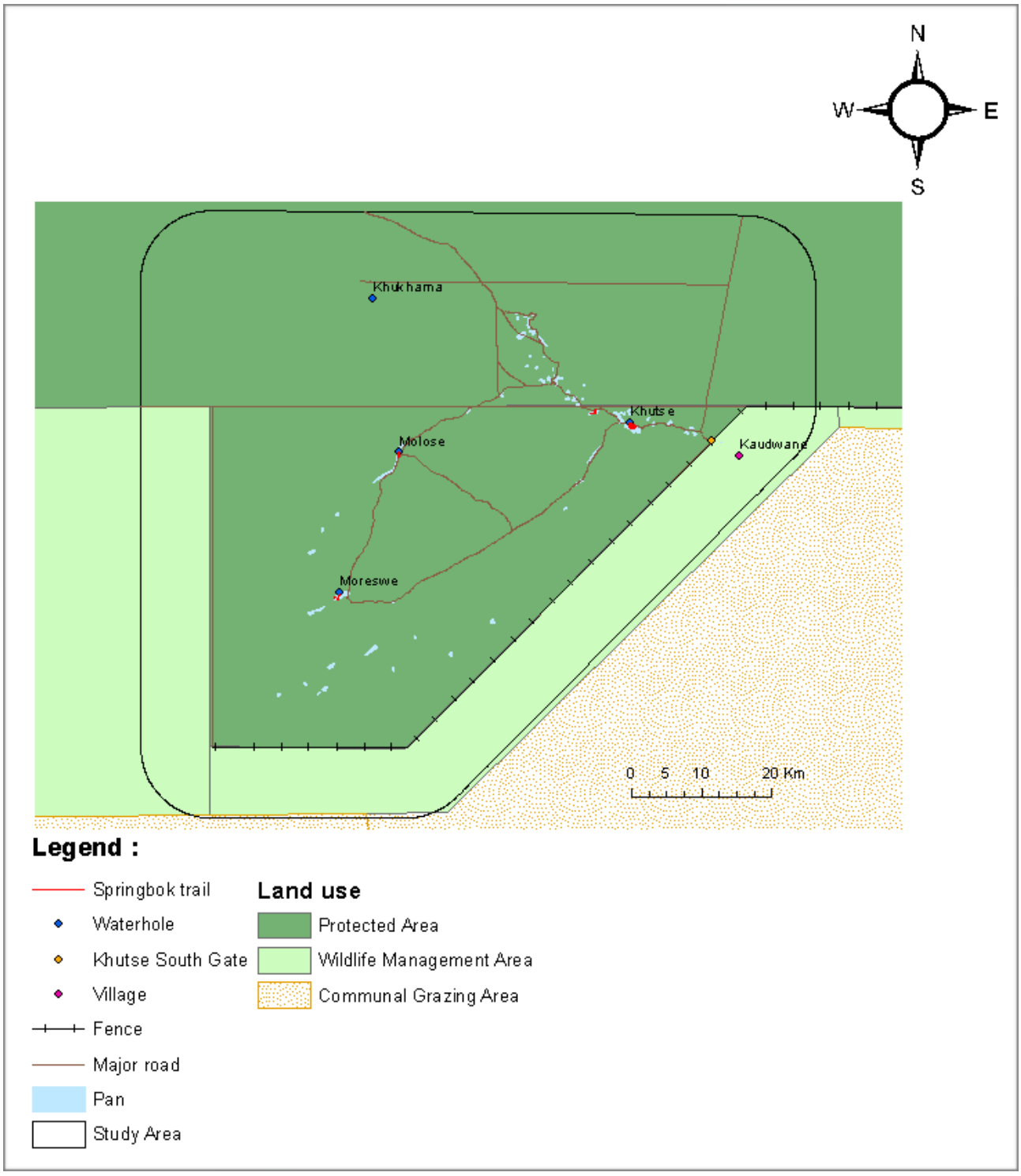


**Figure 9 : Distribution of the 13 Springbok trails collected in Khutse Game Reserve, Kalahari, Botswana, and used for the analysis**

- **For the ostriches trail :**

For this species, we identified only one unbiased trail. This was not enough to calculate an average DTD estimate and its standard deviation for unbiased trails, in order to test the inclusion of biased trails in the final dataset. So, we corrected any biased trail eligible to do so and assumed that the corrected trails and eligible « estimation » trails were sufficiently reliable to be included in the final dataset.

Out of the nine biased trails recorded for ostriches, five were « incomplete » and could not be corrected because they lacked too many hours of the minimum of 22 hours required. Therefore, they were discarded from the final dataset.

Amongst the other four biased trails, one « incomplete » trail and one « running » trail could be corrected (using the same methods as before). Together with the one unbiased trail and two « estimation » trails, they were included in the final dataset.

**Table 14 : Dataset of ostrich trails : presentation of potential biases, correction of daily travel distance values, and inclusion in the final dataset**

| Trail length (km) | Trail quality | Biased trail category | Corrected trail length (km) | Inclusion in final dataset | Reason of inclusion |
|---|---|---|---|---|---|
| 2.799 | Biased | Estimation | 2.799 | Yes | |
| 3.050 | Biased | Incomplete, Estimation | 3.183 | Yes | |
| 3.363 | Biased | Estimation | 3.363 | Yes | |
| 1.933 | Biased | Incomplete | 1.933 | No | Too many missing hours, too much uncertainly in the trail age estimation |
| 2.853 | Biased | Incomplete, Estimation | 2.853 | No | Too many missing hours, too much uncertainly in the trail age estimation |

| | | | | | |
|---|---|---|---|---|---|
| 3.396 | Biased | Incomplete, Estimation | 3.396 | No | Too many missing hours, too much uncertainly in the trail age estimation |
| 8.217 | Biased | Incomplete, Estimation | 8.217 | No | Too many missing hours, too much uncertainly in the trail age estimation |
| 7.998 | Unbiased | | 7.998 | Yes | |
| 8.571 | Biased | Running | 8.430 | Yes | |
| 5.361 | Biased | Incomplete | 5.361 | No | Too many missing hours, too much uncertainly in the trail age estimation |

With all the trailings we kept (5) (Table 14), we calculated the final DTD estimate average, the standard deviation, the standard error and the 95% confidence interval (Table 15).

**Table 15 : Summary of the average DTD and the measures of data dispersion around it for the ostrichs**

| | |
|---|---|
| **Allometric DTD estimate (km)** | 3.05 |
| **Final empirical average DTD estimate (km)** | **5.155** |
| **Standard deviation of the empirical average DTD estimate (km)** | 2.804 |
| **Standard error of the empirical average DTD estimate (km)** | 1.254 |
| **95% Confidence interval around the empirical average DTD estimate** | 2.458 |

The difference between the allometric (3.05 km) and empirical (5.155 km) estimates of the average DTD is substantial. Indeed, the empirical estimate is 1.69 time greater than the allometric estimate.

A map of the various ostrich trails retained in the final dataset has been produced (Figure 10) to give a better idea of their distribution in Khutse Game Reserve.

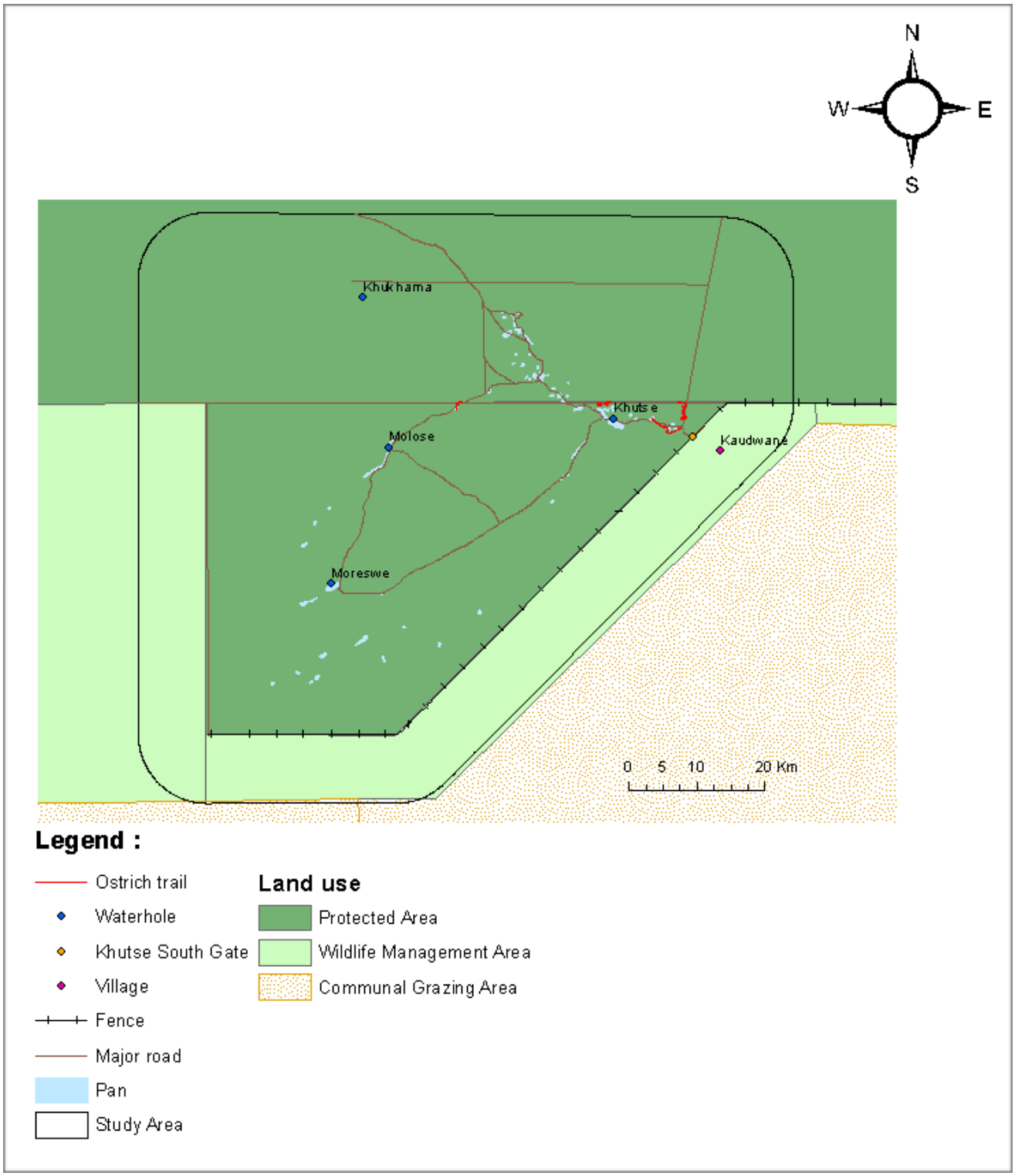


**Figure 10 : Distribution of the 5 Ostrich trails collected in Khutse Game Reserve, Kalahari, Botswana, and used for the analysis**

## b) Verification of data normality

First, we did the standardization on the unbiased datasets of trails, for all species together, to check the normality of its data and calculated the average DTD estimate and its dispersion parameters.
To do this, we used a Shapiro test and created a Q-Q plot.

According to the results (Figures 11), data are normality distributed. We obtained a W-statistic equal to 0.97 and a p-value of 0.31.

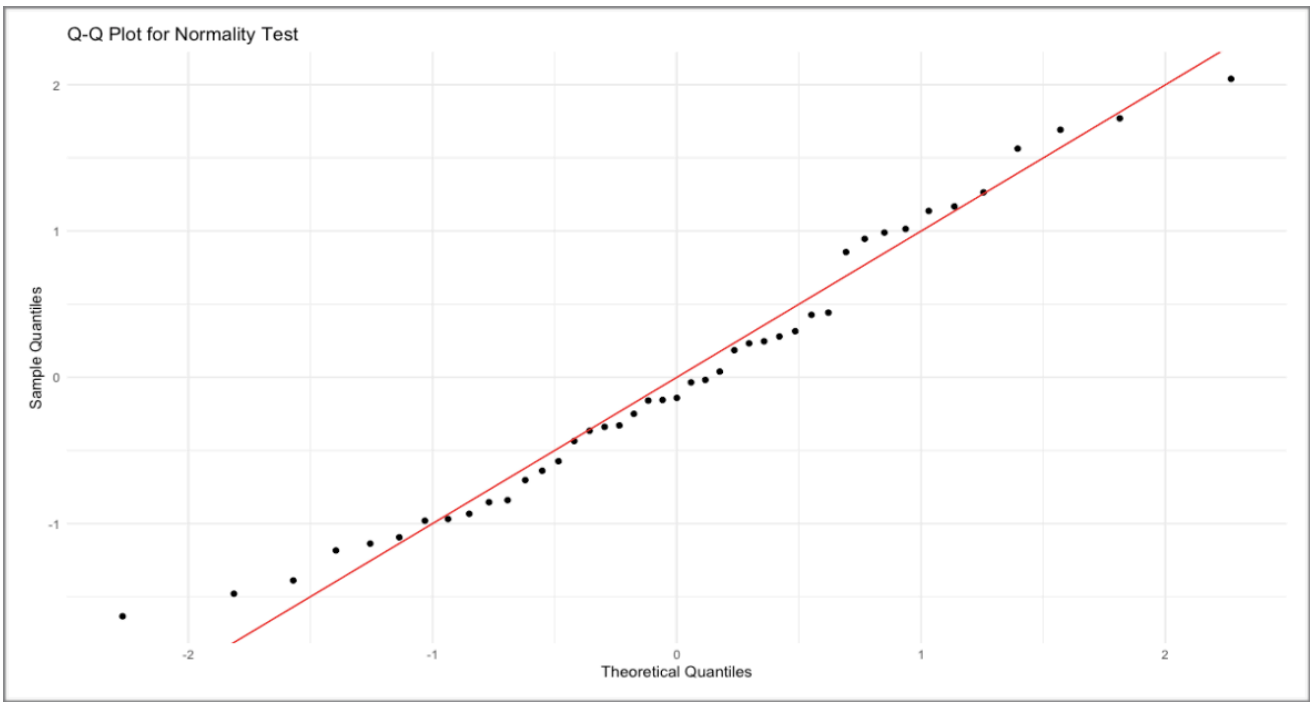


**Figure 11 : Q-Q plot of standardized residuals (unbiased trails)**

We were therefore confident in performing the calculations for the average DTD and the measures of data dispersion around it for each species.
Then we did the same operation with the final dataset (i.e. unbiased trails and corrected trails that were retained), for all species together. According to the results (Figures 12), data are normality distributed. We obtained a W-statistic equal to 0.96 and a p-value of 0.07.

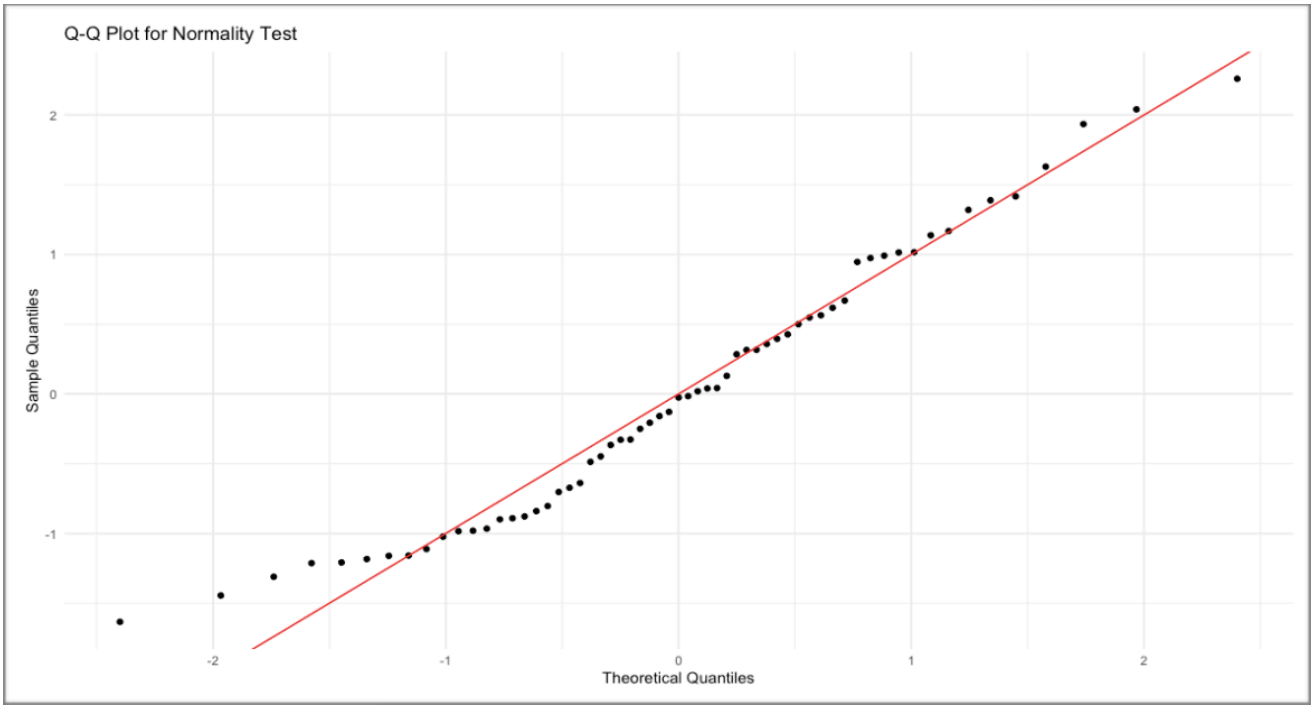


**Figure 12 : Q-Q plot of standardized residuals (unbiased and corrected trails)**

So all the calculations (the average and the measures of data dispersion around it) could be carried out without any problems.

## 2) Effect of group size on DTD

The Table 16 shows the data values obtained after ranking DTD and group size variables, followed by data standardization.

**Table 16 : DTD and group size data for the four species (eland, red hartebeest, greater kudu and springbok)**

| Species | Corrected DTD (km) | DTD's rank | Standardized of ranked DTD | Number of individuals | Group's rank | Standardized ranked group |
|---|---|---|---|---|---|---|
| Eland | 10, 673 | 7 | -1.664 | 50+ | 10.5 | -0.682 |
| Eland | 6.113 | 4 | -2.496 | 10 | 6 | -1.932 |
| Eland | 19.832 | 12 | -0.277 | 5 | 4 | -2.488 |
| Eland | 17.188 | 11 | -0.555 | 100+ | 12 | -0.265 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Eland | 12.89 | 9 | -1.109 | 30 | 9 | -1.099 |
| Eland | 4.856 | 1 | -3.328 | 50+ | 10.5 | -0.682 |
| Eland | 5.514 | 3 | -2.773 | 15 | 7 | -1.654 |
| Eland | 8.298 | 5 | -2.219 | 17 | 8 | -1.377 |
| Eland | 9.841 | 6 | -1.941 | 9 | 5 | -2.210 |
| Eland | 13.123 | 10 | -0.832 | 3 | 3 | -2.766 |
| Eland | 12.2 | 8 | -1.387 | 2 | 2 | -3.044 |
| Eland | 5.086 | 2 | -3.051 | 1 | 1 | -3.321 |
| Hartebeest | 3.027 | 4 | -2.867 | 12 | 11.5 | -0.788 |
| Hartebeest | 5.79 | 7 | -2.097 | 4 | 3 | -3.020 |
| Hartebeest | 10.466 | 12 | -0.813 | 5 | 5 | -2.495 |
| Hartebeest | 11.162 | 13 | -0.556 | 10 | 8.5 | -1.576 |
| Hartebeest | 9.162 | 11 | -1.07 | 12 | 11.5 | -0.788 |
| Hartebeest | 6.266 | 9 | -1.583 | 7 | 6.5 | -2.101 |
| Hartebeest | 1.881 | 2 | -3.381 | 12 | 11.5 | -0.788 |
| Hartebeest | 9.026 | 10 | -1.327 | 4 | 3 | -3.020 |
| Hartebeest | 4.774 | 6 | -2.354 | 7 | 6.5 | -2.101 |
| Hartebeest | 4.253 | 5 | -2.611 | 2 | 1 | -3.545 |
| Hartebeest | 2.933 | 3 | -3.124 | 10 | 8.5 | -1.576 |
| Hartebeest | 1.124 | 1 | -3.638 | 4 | 3 | -3.020 |
| Hartebeest | 5.904 | 8 | -1.840 | 12 | 11.5 | -0.788 |
| Kudu | 7.171 | 13 | -2.903 | 7 | 13 | -2.903 |
| Kudu | 3.566 | 5 | -4.402 | 1 | 5 | -4.402 |
| Kudu | 4.255 | 7 | -4.027 | 1 | 7 | -4.027 |
| Kudu | 6.51 | 10 | -3.465 | 10 | 10 | -3.465 |
| Kudu | 8.177 | 16 | -2.341 | 3 | 16 | -2.341 |
| Kudu | 6.586 | 11 | -3.278 | 6 | 11 | -3.278 |
| Kudu | 3.773 | 6 | -4.215 | 12 | 6 | -4.215 |
| Kudu | 5.78 | 9 | -3.653 | 1 | 9 | -3.653 |
| Kudu | 2.752 | 1 | -5.151 | 4 | 1 | -5.151 |
| Kudu | 11.168 | 18 | -1.967 | 4 | 18 | -1.967 |
| Kudu | 6.774 | 12 | -3.091 | 4 | 12 | -3.091 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Kudu | 5.354 | 8 | -3.840 | 3 | 8 | -3.840 |
| Kudu | 8.951 | 17 | -2.154 | 5 | 17 | -2.154 |
| Kudu | 2.995 | 2 | -4.963 | 2 | 2 | -4.964 |
| Kudu | 7.296 | 14 | -2.716 | 6 | 14 | -716 |
| Kudu | 3.105 | 3 | -4.777 | 4 | 3 | -4.777 |
| Kudu | 7.419 | 15 | -2.529 | 6 | 15 | -2.529 |
| Kudu | 3.522 | 4 | -4.589 | 6 | 4 | -4.589 |
| Springbok | 2.411 | 12 | -0.813 | 35 | 11.5 | -0.885 |
| Springbok | 1.591 | 4 | -2.867 | 43 | 13 | -0.492 |
| Springbok | 2.903 | 13 | -0.556 | 26 | 9 | -1.531 |
| Springbok | 2.306 | 11 | -1.07 | 35 | 11.5 | -0.885 |
| Springbok | 2.023 | 10 | -1.327 | 4 | 3 | -3.085 |
| Springbok | 1.145 | 2 | -3.381 | 4 | 3 | -3.085 |
| Springbok | 1.812 | 8 | -1.840 | 4 | 3 | -3.085 |
| Springbok | 1.654 | 6 | -2.354 | 7 | 5.5 | -2.438 |
| Springbok | 1.704 | 7 | -2.097 | 17 | 8 | -1.791 |
| Springbok | 0.899 | 1 | -3.638 | 7 | 5.5 | -2.438 |
| Springbok | 1.256 | 3 | -3.124 | 14 | 7 | -2.05 |
| Springbok | 1.611 | 5 | -2.611 | 3 | 1 | -3.603 |
| Springbok | 1.962 | 9 | -1.583 | 33 | 10 | 1.273 |

The Figure 13 shows the linear regressions, for each of the 4 species (eland, hartebeest, greater kudu and springbok), of the standardized ranked DTD as function of standardized ranked group size.

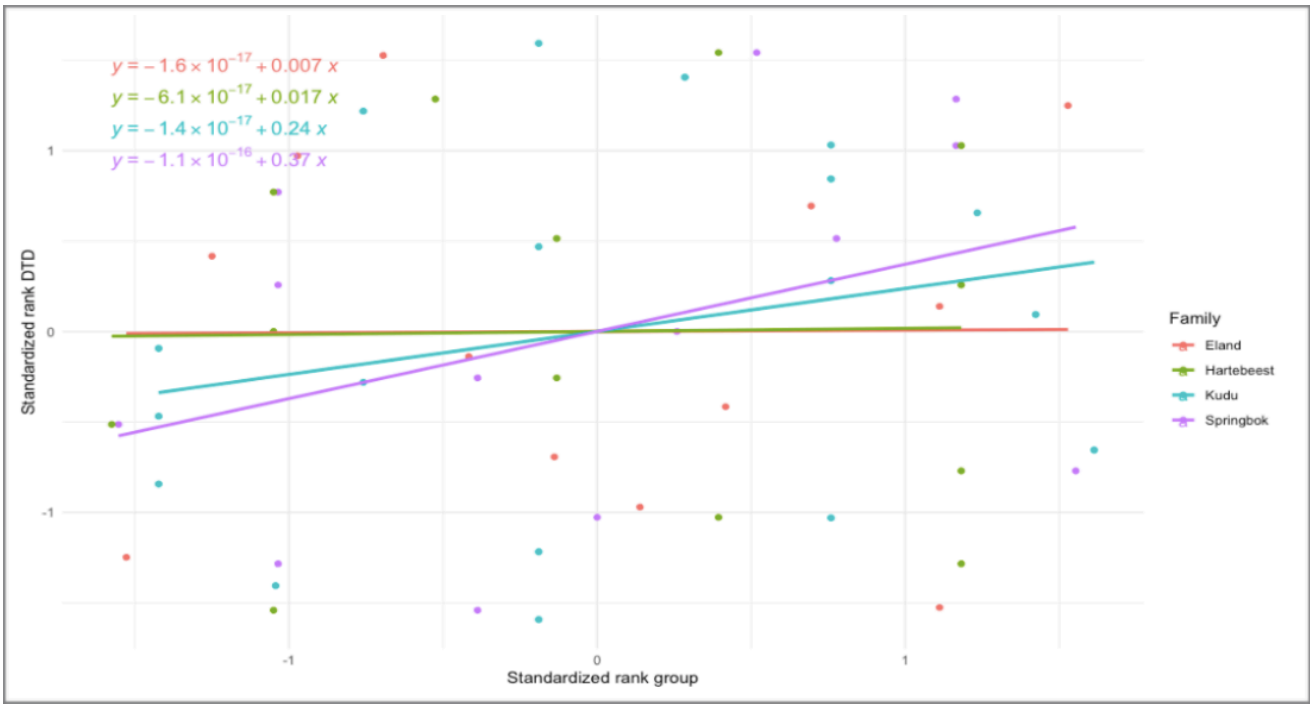


**Figure 13 : The standardized rank DTD as function of the standardized rank group**

**Table 17 : Results of the regression of the effect of the group size on the DTD**

| Variables | Estimate | Standard error | t-value | p-value |
|---|---|---|---|---|
| Intercept | 5.004E-18 | 1.293E-01 | 0 | 1 |
| Centrerankgroup | 1.686E-01 | 1.341E-01 | 1.257 | 0.214 |

In each case, the slope of the line is positive. This means, that DTD increase with the size of the group. But, as Table 17 shows that even if the coefficients are estimated as positive numbers they are not significantly different from 0.

The results of the ANOVA applied on the linear regression of the standardized group's rank variable on the standardized DTD's rank shows that the p-values are not significant (Table 18).

**Table 18 : Results of the ANOVA of the effect of the group size on the DTD**

| Variables | Degree of freedom | Sum squares | Mean squares | F-statictic | p-value | Significance of results |
|---|---|---|---|---|---|---|
| Species | 3 | 0.00 | 0.0000 | 0.000 | 1.000 | Not significant |

| | | | | | | |
|---|---|---|---|---|---|---|
| Centrerankgroup | 1 | 1.48 | 1.4786 | 1.437 | 0.236 | Not significant |
| Species * Centrerankgroup | 3 | 1.14 | 0.3788 | 0.368 | 0.776 | Not significant |

With the necessary assumptions verified, we were able to validate our model (see the Appendix 4).
In view of our results, there is not enough evidence that the group size influence DTD. This means that the unexplained variance observed between points may then be due to other variables not included in the model but can interact with the effect of group size on DTD. In our case, the other variables not included can be defined as other natural events (e.g. wind, full moon, predators, etc.) but also many other variables linked to the species that we did not test.
Therefore, based on our dataset only, the conclusion is that group size has no effect on DTD. But, since the sample size of our dataset is small, it might be just a case that the effect, if it exists, is too small to be detected.

## 3) Effect of sex on DTD

The Table 19 shows the sexual composition (male, female or mixed) of the group monitored for each DTD.

**Table 19 : DTD and sex data for the four species (eland, red hartebeest, greater kudu and springbok)**

| Speies | DTD (km) | Sex |
|---|---|---|
| Eland | 10.673 | Mixed |
| Eland | 6.113 | Mixed |
| Eland | 19.832 | Mixed |
| Eland | 17.188 | Mixed |
| Eland | 12.89 | Mixed |
| Eland | 4.856 | Mixed |
| Eland | 5.514 | Mixed |
| Eland | 8.298 | Female |
| Eland | 9.841 | Female |

| | | |
|---|---|---|
| Eland | 13.123 | Mixed |
| Eland | 12.2 | Male |
| Eland | 5.086 | Female |
| Hartebeest | 3.217 | Mixed |
| Hartebeest | 5.79 | Mixed |
| Hartebeest | 10.466 | Mixed |
| Hartebeest | 11.162 | Mixed |
| Hartebeest | 9.026 | Mixed |
| Hartebeest | 6.266 | Mixed |
| Hartebeest | 1.881 | Mixed |
| Hartebeest | 9.026 | Mixed |
| Hartebeest | 4.774 | Mixed |
| Hartebeest | 4.253 | Male |
| Hartebeest | 2.933 | Mixed |
| Hartebeest | 1.124 | Mixed |
| Hartebeest | 5.904 | Mixed |
| Kudu | 7.171 | Mixed |
| Kudu | 3.566 | Mixed |
| Kudu | 4.255 | Male |
| Kudu | 6.51 | Mixed |
| Kudu | 8.177 | Mixed |
| Kudu | 6.586 | Mixed |
| Kudu | 3.773 | Mixed |
| Kudu | 5.78 | Male |
| Kudu | 2.752 | Mixed |
| Kudu | 11.168 | Mixed |
| Kudu | 6.774 | Female |
| Kudu | 5.354 | Male |
| Kudu | 8.951 | Mixed |
| Kudu | 2.995 | Male |
| Kudu | 7.296 | Mixed |
| Kudu | 3.105 | Female |

| | | |
|---|---|---|
| Kudu | 7.419 | Female |
| Kudu | 3.522 | Mixed |
| Springbok | 2.411 | Mixed |
| Springbok | 1.591 | Mixed |
| Springbok | 2.903 | Mixed |
| Springbok | 2.306 | Mixed |
| Springbok | 2.023 | Mixed |
| Springbok | 1.145 | Mixed |
| Springbok | 1.812 | Mixed |
| Springbok | 1.654 | Mixed |
| Springbok | 1.704 | Mixed |
| Springbok | 0.899 | Mixed |
| Springbok | 1.256 | Mixed |
| Springbok | 1.611 | Female |
| Springbok | 1.962 | Mixed |

The results of the two-way ANOVA testing the effect of the sex structure variable on the DTD shows that the results are not significant (apart from the difference in DTDs between the species) (Table 20).

**Table 20 : Results of the ANOVA testing the effect of the sex on DTD**

| Variables | Degree of freedom | Sum squares | Mean squares | F-statistic | p-values | Significance of results |
|---|---|---|---|---|---|---|
| Species | 3 | 470.0 | 156.67 | 16.307 | 2.34E-07 | Significant |
| Sex | 2 | 21.1 | 10.54 | 1.097 | 0.343 | Not significant |
| Species * Sex | 4 | 20.9 | 5.22 | 0.544 | 0.705 | Not significant |

With the assumptions verified, we were able to validate our model (see Appendix 5).

So, there is no effect of sex on DTD or the effect is not strong enough to be detected with this limited dataset.

## 4) Effect of the social structure on DTD

The Table 21 shows the social structure (« adults », without subadults and juveniles, and « family », with subadults and juveniles) of the individual (in our dataset, the single individuals were only adults) or the group sampled.

**Table 21 : DTD and social structure data for the five species**

| Speies | DTD (km) | Social structure |
|---|---|---|
| Eland | 10.673 | Family |
| Eland | 6.113 | Family |
| Eland | 19.832 | Adults |
| Eland | 17.188 | Family |
| Eland | 12.89 | Family |
| Eland | 4.856 | Family |
| Eland | 5.514 | Family |
| Eland | 8.298 | Family |
| Eland | 9.841 | Family |
| Eland | 13.123 | Family |
| Eland | 12.2 | Adults |
| Eland | 5.086 | Adults |
| Hartebeest | 3.217 | Family |
| Hartebeest | 5.79 | Adults |
| Hartebeest | 10.466 | Family |
| Hartebeest | 11.162 | Family |
| Hartebeest | 9.026 | Family |
| Hartebeest | 6.266 | Family |
| Hartebeest | 1.881 | Family |
| Hartebeest | 9.026 | Adults |
| Hartebeest | 4.774 | Family |
| Hartebeest | 4.253 | Adults |
| Hartebeest | 2.933 | Family |

| | | |
|---|---|---|
| Hartebeest | 1.124 | Family |
| Hartebeest | 5.904 | Family |
| Kudu | 7.171 | Family |
| Kudu | 3.566 | Adults |
| Kudu | 4.255 | Adults |
| Kudu | 6.51 | Family |
| Kudu | 8.177 | Family |
| Kudu | 6.586 | Family |
| Kudu | 3.773 | Family |
| Kudu | 5.78 | Adults |
| Kudu | 2.752 | Family |
| Kudu | 11.168 | Family |
| Kudu | 6.774 | Adults |
| Kudu | 5.354 | Family |
| Kudu | 8.951 | Family |
| Kudu | 2.995 | Adults |
| Kudu | 7.296 | Family |
| Kudu | 3.105 | Family |
| Kudu | 7.419 | Adults |
| Kudu | 3.522 | Family |
| Springbok | 2.411 | Family |
| Springbok | 1.591 | Family |
| Springbok | 2.903 | Adults |
| Springbok | 2.306 | Family |
| Springbok | 2.023 | Adults |
| Springbok | 1.145 | Family |
| Springbok | 1.812 | Adults |
| Springbok | 1.654 | Adults |
| Springbok | 1.704 | Family |
| Springbok | 0.899 | Family |
| Springbok | 1.256 | Family |
| Springbok | 1.611 | Adults |

| | | |
|---|---|---|
| Springbok | 1.962 | Family |
| Ostrich | 2.799 | Adults |
| Ostrich | 3.183 | Adults |
| Ostrich | 3.363 | Adults |
| Ostrich | 7.998 | Family |
| Ostrich | 8.43 | Family |

The results of the two-way ANOVA of the social structure variable on the DTD shows that the results are not significant (apart from the difference in DTDs between the species) (Table 22).

**Table 22 : Results of the ANOVA testing the effect of the social structure on DTD**

| Variables | Degree of freedom | Sum squares | Mean squares | F-statistic | p-values | Significance of results |
|---|---|---|---|---|---|---|
| Species | 4 | 19.414 | 4.854 | 20.701 | 3.49E-10 | Significant |
| Demography | 1 | 0.001 | 0.001 | 0.003 | 0.959 | Not significant |
| Species * Demography | 4 | 1.622 | 0.406 | 1.730 | 0.158 | Not significant |

With the assumptions verified, we were able to validate our model (see Appendix 6).
So, there is no effect of the social structure on DTD or the effect is not strong enough to be detected with this limited dataset.

## 5) Effect of temporal progress in the dry season on DTD

Another interesting aspect we studied is the possible variation in DTD throughout across the dry season for the different species.
We numbered the days starting from the first trailing to the last one, as shown in Table 23.

**Table 23 : Number of days from the start of the project and DTD for the five species**

| Speies | DTD (km) | Date | Number of days |
|---|---|---|---|

| | | | |
|---|---|---|---|
| Eland | 10.673 | 18/05/2023 | 3 |
| Eland | 6.113 | 28/06/2023 | 44 |
| Eland | 19.832 | 11/07/2023 | 57 |
| Eland | 17.188 | 12/07/2023 | 58 |
| Eland | 12.89 | 21/07/2023 | 67 |
| Eland | 4.856 | 25/07/2023 | 71 |
| Eland | 5.514 | 31/07/2023 | 77 |
| Eland | 8.298 | 01/08/2023 | 78 |
| Eland | 9.841 | 02/08/2023 | 79 |
| Eland | 13.123 | 03/08/2023 | 80 |
| Eland | 12.2 | 08/08/2023 | 85 |
| Eland | 5.086 | 10/08/2023 | 87 |
| Hartebeest | 3.217 | 16/05/2023 | 1 |
| Hartebeest | 5.79 | 23/05/2023 | 8 |
| Hartebeest | 10.466 | 26/05/2023 | 11 |
| Hartebeest | 11.162 | 30/05/2023 | 15 |
| Hartebeest | 9.026 | 02/06/2023 | 18 |
| Hartebeest | 6.266 | 08/06/2023 | 24 |
| Hartebeest | 1.881 | 12/06/2023 | 28 |
| Hartebeest | 9.026 | 13/06/2023 | 29 |
| Hartebeest | 4.774 | 14/06/2023 | 30 |
| Hartebeest | 4.253 | 23/06/2023 | 39 |
| Hartebeest | 2.933 | 29/06/2023 | 45 |
| Hartebeest | 1.124 | 10/07/2023 | 56 |
| Hartebeest | 5.904 | 13/07/2023 | 59 |
| Kudu | 7.171 | 24/05/2023 | 9 |
| Kudu | 3.566 | 25/05/2023 | 10 |
| Kudu | 4.255 | 15/06/2023 | 31 |
| Kudu | 6.51 | 19/06/2023 | 35 |
| Kudu | 8.177 | 21/06/2023 | 37 |
| Kudu | 6.586 | 21/07/2023 | 37 |
| Kudu | 3.773 | 22/06/2023 | 38 |

| | | | |
|---|---|---|---|
| Kudu | 5.78 | 26/06/2023 | 42 |
| Kudu | 2.752 | 05/07/2023 | 51 |
| Kudu | 11.168 | 19/07/2023 | 65 |
| Kudu | 6.774 | 27/07/2023 | 73 |
| Kudu | 5.354 | 29/07/2023 | 75 |
| Kudu | 8.951 | 04/08/2023 | 81 |
| Kudu | 2.995 | 07/08/2023 | 84 |
| Kudu | 7.296 | 09/08/2023 | 86 |
| Kudu | 3.105 | 11/08/2023 | 88 |
| Kudu | 7.419 | 14/08/2023 | 91 |
| Kudu | 3.522 | 15/08/2023 | 92 |
| Springbok | 2.411 | 17/05/2023 | 2 |
| Springbok | 1.591 | 22/05/2023 | 7 |
| Springbok | 2.903 | 31/05/2023 | 16 |
| Springbok | 2.306 | 05/06/2023 | 21 |
| Springbok | 2.023 | 09/06/2023 | 25 |
| Springbok | 1.145 | 20/06/2023 | 36 |
| Springbok | 1.812 | 27/06/2023 | 43 |
| Springbok | 1.654 | 04/07/2023 | 50 |
| Springbok | 1.704 | 06/07/2023 | 52 |
| Springbok | 0.899 | 10/07/2023 | 56 |
| Springbok | 1.256 | 20/07/2023 | 66 |
| Springbok | 1.611 | 20/07/2023 | 66 |
| Springbok | 1.962 | 26/07/2023 | 72 |
| Ostrich | 2.799 | 19/05/2023 | 4 |
| Ostrich | 3.183 | 29/05/2023 | 14 |
| Ostrich | 3.363 | 01/06/2023 | 17 |
| Ostrich | 7.998 | 07/07/2023 | 53 |
| Ostrich | 8.43 | 24/07/2023 | 70 |

With the necessary assumptions verified, we were able to apply an lm (see Appendix 7).

The results of the linear model of the effect of the temporal progress in the dry season variable on the DTD shows that only the interaction between ostriches and the temporal progress in the dry season is significant (apart from the difference of intercept between the species) (Table 24).

**Table 24 : Results of the effect of the temporal progress in the dry season on DTD**

| Variables | Estimate | Standard Error | t-values | p-values | Significance of results |
|---|---|---|---|---|---|
| Intercept | 2.496242 | 0.410799 | 6.077 | 1.56E-07 | Significant |
| Species Hartebeest | -0.424175 | 0.477645 | -0.888 | 0.37868 | Not significant |
| Species Kudu | -0.805129 | 0.482515 | -1.669 | 0.10132 | Not significant |
| Species Ostrich | -1.562047 | 0.526773 | -2.965 | 0.00459 | Significant |
| Species Springbok | -1.686008 | 0.485058 | -3.476 | 0.00105 | Significant |
| Number of days | -0.003812 | 0.005933 | -0.643 | 0.52337 | Not significant |
| Species Hartebeest * Number of days | -0.013792 | 0.009505 | -1.451 | 0.15292 | Not significant |
| Species Kudu * Number of days | 0.003695 | 0.007163 | 0.516 | 0.60817 | Not significant |
| Species Ostrich * Number of days | 0.022419 | 0.010071 | 2.226 | 0.03044 | Significant |
| Species Springbok * Number of days | -0.003111 | 0.008217 | -0.379 | 0.70659 | Not significant |

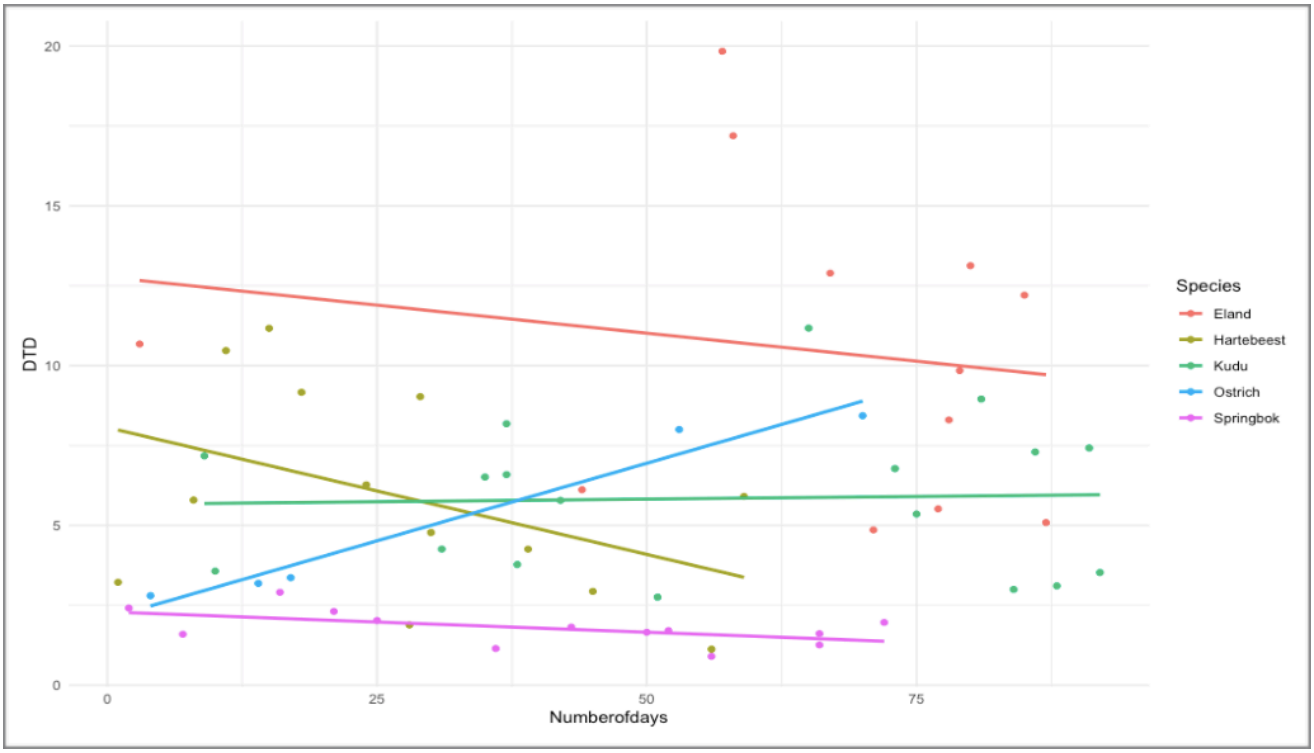


**Figure 14 : The effect of the number of days from the start of the project on DTD**

Table 14 indeed illustrates the results of the linear regression for ostriches, which display an increase in DTDs as the dry season progresses.

In the case of elands, red hartebeests and springboks, there seems to be a slight decrease in DTDs with time, and the opposite for the greater kudus. But this effect, if it exists, is probably not strong enough to be significant with our limited sample size.

## 6) Prediction of empirical average DTD estimate in function of allometric average DTD estimate.

Table 25 shows the allometric and empirical average DTD estimate for various species belonging to the Artiodactyla and Carnivora orders.

**Table 25 : Allometric and empirical average DTD estimate for various species**

| Species | Order | Allometric DTD (km) | Empirical DTD (km) | Source empirical DTD |
|---|---|---|---|---|
| Eland | Artiodactyla | 4.64 | 10.468 | |
| Kudu | Artiodactyla | 3.6 | 5.842 | |
| Hartebeest | Artiodactyla | 3.36 | 5.843 | |

| | | | | |
|---|---|---|---|---|
| Springbok | Artiodactyla | 2.31 | 1.79 | |
| Ostrich | Artiodactyla | 3.05 | 5.155 | |
| Gemsbok | Artiodactyla | 3.58 | 5.6 | D. Keeping (unpubl. data) |
| Wildebeest | Artiodactyla | 3.62 | 7.063 | Selebatso et al. (2018) |
| Steenbok | Artiodactyla | 1.69 | 4.5 | D. Keeping (unpubl. data) |
| Brown Hyena | Carnivora | 5.88 | 31.1 | Mills (1990) |
| Cheetah | Carnivora | 6.01 | 9 | M. G. L. Mills (unpubl. data) |
| Leopard | Carnivora | 6.26 | 9.7 | Stander (1998) |
| Lion | Carnivora | 10.27 | 19.4 | Stander (1998) |
| Spotted Hyena | Carnivora | 6.72 | 26.5 | Mills (1990) |
| Honey Badger | Carnivora | 3.24 | 10.8 | Begg et al. (2005) |
| Yellow mongoose | Carnivora | 0.95 | 3.2 | Cavallini (1993) |
| Aardvark | Carnivora | 6.54 | 8.6 | D. Keeping (unpubl. data) |
| Ground Pangolin | Carnivora | 3.35 | 3.8 | Skinner & Chimimba (2005) |

To begin our analysis, we checked the scatterplot of the relationship between empirical and allometric data for all species combined (Figure 15).

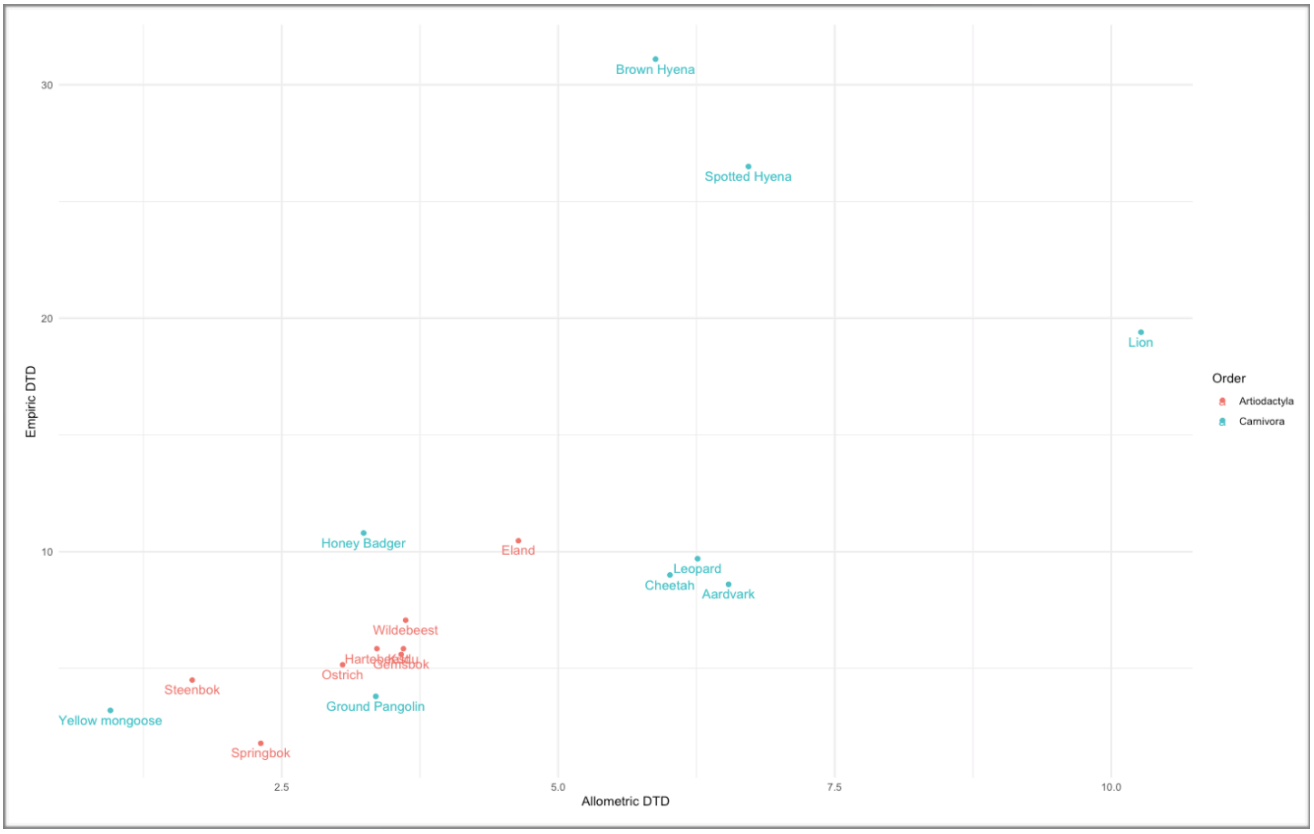


**Figure 15 : Scatterplot of empirical average DTD estimate as function of the allometric average DTD estimate for the Artiodactyla and the Carnivora orders**

Looking at the Figure 15 gathering all observations, there appears to have no clear shape to the relationship between empirical average DTD estimate and allometric average DTD estimate. For Artiodactyla order alone, there seems to be more and less linear increase of empirical average DTD estimate following an increase of allometric average DTD estimate.

In the case of Carnivora, we noticed that the data for brown and spotted hyenas are diverging strongly from the other Carnivora observations. This divergence is probably due to the behavior of these two species, so we have chosen to consider them as outliers, but from an ecological point of view. We therefore ran a scatterplot without the data for the two hyena species, and the shape of the relationship appeared more linear. We have therefore decided to consider hyenas as outliers and not to take them into account when establishing our correction coefficient (Figure 16).

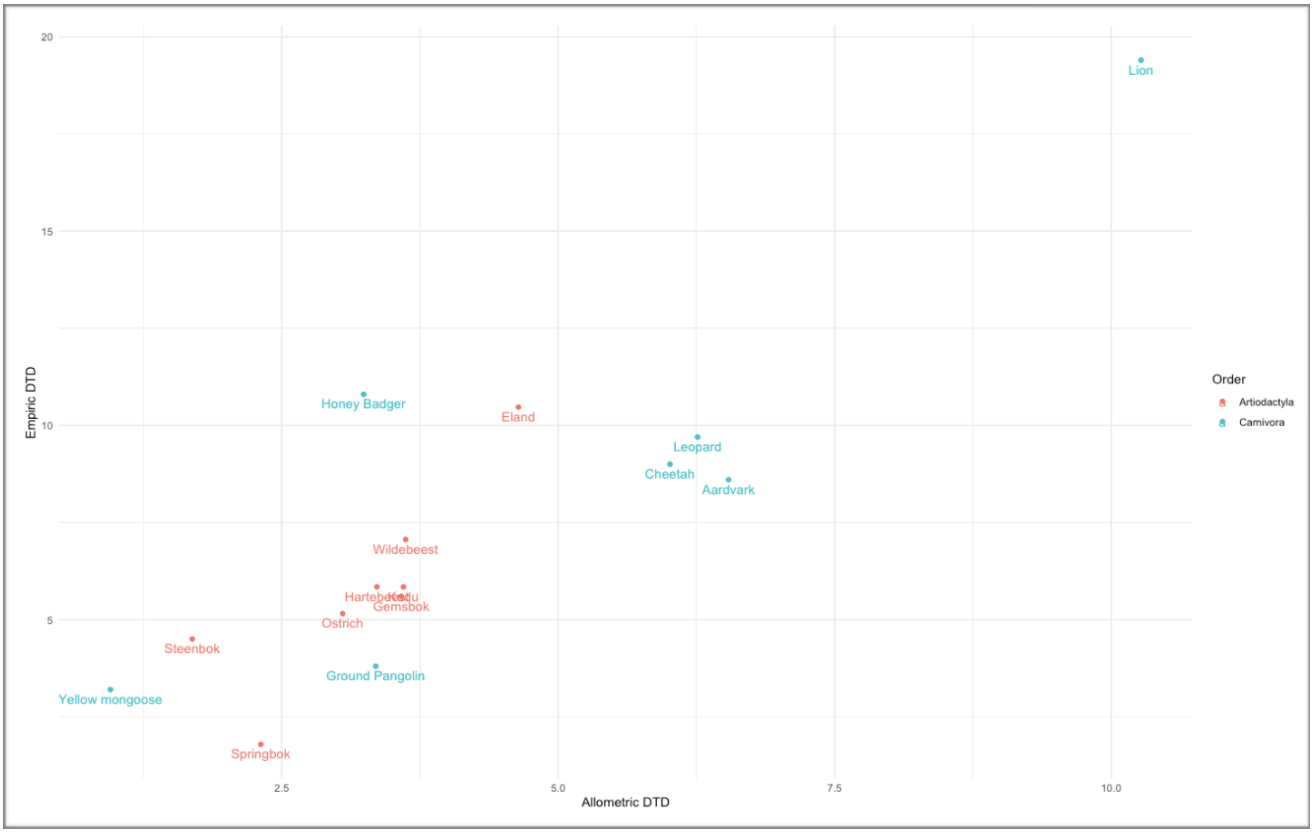


**Figure 16 : Graph of empirical average DTD estimate as function of the allometric average DTD estimate for the Artiodactyla and the Carnivora orders (without the brown hyena and the spotted hyena)**

Once our final dataset was defined, we applied a linear model based on the relationship between empirical average DTD estimates and allometric average DTD estimates, with orders (Artiodactyla and Carnivora) and with the interaction between allometric average DTD estimates and orders.
When we checked the assumptions required to apply an lm, we realized although diagnostic plots show a slight deviation from linearity, this is likely to be an artefact due to small sample size, as no apparent shape emerges from the points distribution (see Appendix 8). We therefore decided to keep the linear model.

**Table 26 : Results of the regression of the empirical average DTD estimate as function of the allometric average DTD estimate for the Artiodactyla and the Carnivora orders (without the brown hyena and the spotted hyena)**

| Variables | Estimate | Standard Error | t-value | p-value | Significance of results |
|---|---|---|---|---|---|

| | | | | | |
|---|---|---|---|---|---|
| Intercept | -1.5348 | 3.1893 | -0.481 | 0.6398 | Not significant |
| Order | 2.7362 | 3.6744 | 0.745 | 0.4721 | Not significant |
| Allometric | 2.2646 | 0.9551 | 2.371 | 0.0371 | Significant |
| Order * Allometric | -0.7329 | 1.0035 | -0.730 | 0.4804 | Not significant |

The results of the linear model show that our intercept is not significantly different from zero. So, we choose to force $\beta_0$ to zero (Table 26).

We also found that the relationship between empirical average DTD estimate and the interaction of allometric average DTD estimate and orders was not significant (Table 26). In this case, we could construct a single general correction factor for both orders combined. However, to be as precise as possible in predicting the average empirical average DTD estimate from the allometric average DTD estimate, we have chosen to build two separate models for each order (Figures 17 and 18). Therefore, we applied a regression on our data for each order separately under the form of the following equation : Empiric average DTD estimate = $\beta_1$ * allometric average DTD estimate with $\beta_1$ being our correction coefficient.

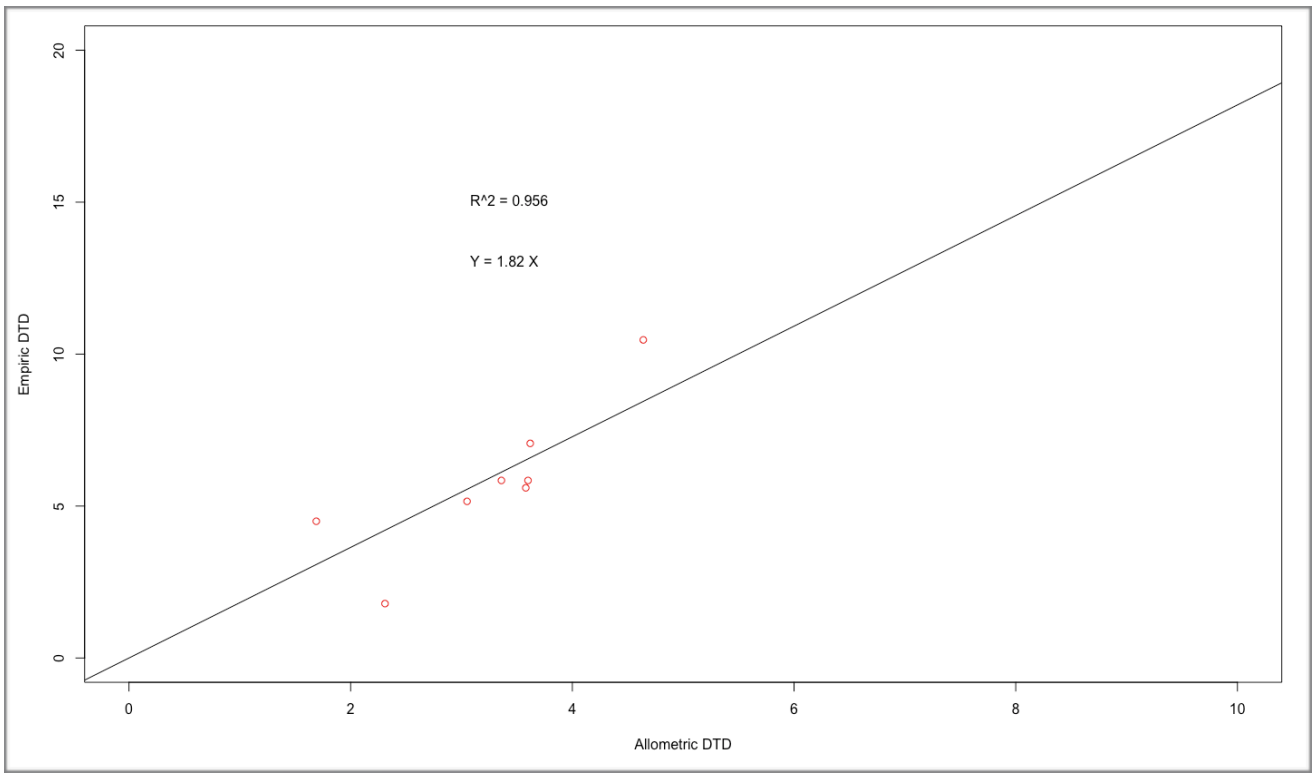


**Figure 17 : Empirical average DTD estimate as function of allometric average DTD estimate for Artiodactyla**

For the Artiodactyla, the final equation is : « empirical average DTD estimate » = 1.82 * « allometric average DTD estimate ». We also have a high $R^2$ of 0.956 (Figure 17), this means that the model is capable of explaining a high percentage of the variability observed in the data. In other words, it means that the model is effective in predicting empirical average DTD estimates from allometric average DTD estimates. So, we can consider the value 1.82 as our correction coefficient for the Artiodactyla.

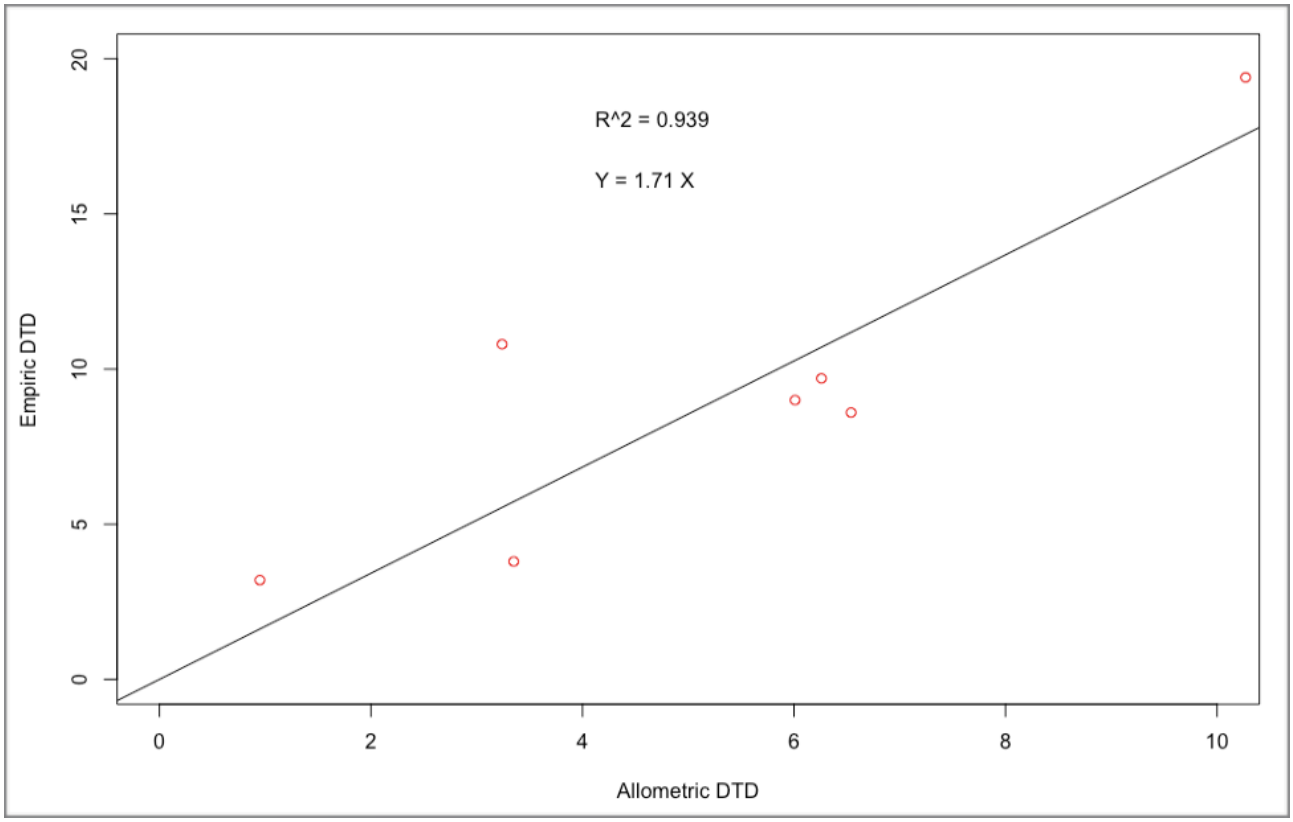


**Figure 18 : Empirical average DTD estimate as function of allometric average DTD estimate for Carnivora**

For the Carnivora, the final equation is : « empiric average DTD estimate » = 1,71 * « allometric average DTD estimate ». We also have a high $R^2$ of 0,939 (Figure 18), this means that model is capable of explaining a high percentage of the variability observed in the data. In other words, it means that the model is effective in predicting empirical average DTD estimates from allometric average DTD estimates. So, we can consider the value 1,71 as our correction coefficient for the Carnivora.

In conclusion, the correction coefficient proposed to correct the estimates of allometric average DTDs for the order Artiodactyla is 1.82 (Figure 17) and for the order Carnivora (except hyena species) it is equal to 1.71 (Figure 18).

# IV. Discussion

The conservation of species has become key for the survival and proper functioning of our planet. The Kalahari Desert landscape deserves protection because it represents one of the largest wilderness areas in Sub-saharan Africa and still hosts a high level of biodiversity. With this in mind, conservation organizations such as LEC seek to assess the population density of different species to provide information needed to design wildlife protection programs.

Here, I investigated further the FMP formula approach, as one of the main wildlife abundance monitoring techniques used in the region. Its primary limitation in yielding accurate density estimates lies in the accuracy of parameter $\hat{M}$, the estimate of the average distance the species travels daily. To address this limitation, I generated empirical average DTD estimates with high spatial resolution for five large herbivore species that previously lacked such data.

When comparing the estimates of allometric and empirical average DTDs for a given species, the difference is relatively large. For instance, using empirical data obtained with the method of the long-follow trailing, our results show that for elands we transition from an allometric estimate of 4.64 km to an empirical estimate of 10.468 km. The difference between the 2 values followed a similar trend for greater kudu, red hartebeest and ostrich and all the other species seen in Table 22 (except springbok).

This difference will be reflected in the density results obtained via the FMP formula. In the FMP formula, a smaller parameter $\hat{M}$ will contribute to having a smaller denominator, which will yield a larger density estimate. Alternatively, while keeping the same values for the other parameters, a larger $\hat{M}$ will give, a larger denominator and therefore a smaller density estimate. For example, on a 15 km transect, 4 eland tracks were seen :

- First, if we use the allometric $\hat{M}$ of this species, we obtain :

$$\widehat{D} = \frac{\pi}{2} \times \frac{x}{S \times \widehat{M}} = \frac{\pi}{2} \times \frac{4}{15 \times 4.64} = 0.09$$

- Secondly, if we use the empirical $\hat{M}$ of the elands, we obtain :

$$\widehat{D} = \frac{\pi}{2} \times \frac{x}{S \times \widehat{M}} = \frac{\pi}{2} \times \frac{4}{15 \times 10.468} = 0.04$$

We find that the allometric average DTD estimate overestimates the population density of the target species. A result that may prove harmful in the decision-making of any related management strategy of the target population.

This difference can be explained by the fact that the allometric estimate does not take into account the animal's behaviour, but only its body mass. Behaviour variables likely explain, for example, the reason for the great difference between allometric and empirical estimates for brown hyenas (the allometric average DTD estimate is equal to 5.88 km while the empirical average DTD estimate is equal to 31.1 km) and even spotted hyenas (the allometric average DTD estimate is equal to 6.72 km while the empirical average DTD estimate is equal to 26.5 km). They are mostly scavengers, so they walk much more than other species to find the food they need (Owens et al., 1978). Hyenas, and spotted hyenas in particular, are also very good hunters. Being social animals, they also need to move around to find prey to feed the pack (Kolowski et al., 2007; Mills, 1989). This particular behaviours are the reason why we decided not to include hyenas in the generation of our correction coefficient.

For springboks, the case is slightly different in that its empirical estimate is lower than the allometric one. During our observations in the field, we noticed that springboks very rarely left the pans in which they had settled. They ate, rested and spent the night in the same place, so they didn't cover as many kilometers as the other herbivores we studied. But, sometimes, some individuals would leave the pans in which they were to go to another pan. We were unable to track these particular events during our field surveys. It is likely that if we had succeeded in collecting trails capturing such traveling behaviour, the average DTD for this species would have been higher. Consequently, the average empirical average DTD estimate for this species should be used with caution. Indeed, despite the fact that these animals stay in the same area most of the time, they may move further. It would therefore be interesting to carry out other long-follows targeting this behavior to get an idea of the distance they might travel and thus improve our empirical average DTD estimate.

In view of our results, the allometric estimate of average DTD, regardless of the species, must be handled with care when used in the Kalahari ecosystem. In most cases, they do not represent the truth and lead to an overestimation of population density.

Using the general correction coefficient, which we managed to generate with all the data for the Artiodactyla (« empirical average DTD estimate » = 1,82 * « allometric average DTD estimate ») and the Carnivora (« empirical average DTD estimate » = 1,71 * « allometric average DTD estimate »), may be a solution to counter this issue if the empirical value is not known. However, it is preferable to use the empirical estimate which, compared to the allometric one, takes into account the behaviour of the target species as well as all intraspecific variation in distance travelled due to the hazards that can occur in nature.

The method we used enabled us to obtain a highly accurate and reliable collection of data. Other techniques, however, might be less reliable depending on the data collection protocol and analysis framework.

So even in the case of an empirical average DTD estimate, one needs to remain critical of the method used and the size of the dataset. For example, in the case of ostriches, we only managed to collect five exploitable trails, which give us a low statistical power to make a robust inference on the average DTD estimate at population level. Trailing ostriches was very complicated because of the soft nature of their feet relative the substrate quality. In fact, when the ground was too hard (often at the level of the pans), the ostrich footprints didn't show. The only detail showing was the ostrich's claw, which is difficult to detect. To remedy this situation, we had to opt for trailing groups of ostriches (to get as many tracks as possible) in sandy areas away from the pans. Another possible solution would have been to track this species outside the reserve, where the ground is sandier and the tracks easier to follow, or in parts of the reserve where there are less pans or calcrete ridges.

One of the reasons why we tried to randomize the trailings we recorded, was to increase the probability to cover a maximum of events that could happen in a large herbivore’s day. Hence, the team has made efforts to sample as many different individuals and areas as possible. This is also the reason why we had set ourselves a minimum of 10 successful trails for each species (in addition to have a minimum of statistical power).

When we talk about « events that could happen », several ideas may come in mind. According to the trackers’ experience, many elements can influence the « habits » of animals and therefore impact their DTD. We observed that during windy and cloudy days, animals walk more as in Wijers et al. (2022) as well. It is possible the decrease of temperatures caused by such weather allows the

animals to move more, especially during the hours when normally they look for shade to mitigate the heat (Berry et al., 2023).

It is also possible, that, during a full moon night, the animals would not necessarily stop to sleep or hide. The light of the moon may favor prey species, because they can see better a predator coming while they are grazing (Lamamy et al., 2021, Prugh et al., 2013).

The presence of predators can also most likely influence preys' DTD. If the prey senses their presence, they may travel less far because they will be more alert and will prefer to save energy if they have to flee (Clark et al., 2017).

We've had trailings that took place during periods of fire in the reserve, trailings where the targeted animals were followed by predators or even attacked while we were on their trail. In addition, we felt it was important to try, to the extent possible, to follow different groups and individuals each time. The natural events that can occur during a trail can modify the distance covered, but it is also possible that other parameters come into play, which characterize the individual or group themselves. These are, for instance, the size of the group, the group's social structure or even it sexual composition.

As the size of the group increases, the individuals in it are naturally expected to walk, on average, longer distances to find the amount of food needed to satisfy everyone's appetite. Even if there is a maximum distance they can cover in a day's time, limited by their energy resources and physical capacity, we expect to see a difference depending on the size of the group. Haoran et al. (2021), for the primate species *Rhinopithecus bieti*, showed that the larger the group, the greater the distance travelled, and vice versa.

But, in large herbivores, research has shown that larger groups can benefit from greater vigilance. This enables them to locate predators and food resources more efficiently, and thus, potentially, not increase the distances they travel (Fortin et al., 2004).

However, when we look at the results we obtained, there is no significant effect of group size on the DTDs for the different species.

This may be due to lack of data. It would be interesting to increase the sample size per species. For our analysis, we chose to test this impact on all the species at the same time because of the limited data we had, but also because the animals studied are all antelopes (here we did not consider ostriches) and their behaviour is expected to be relatively similar. However, we still tested for the interaction between group size and species so we could still test if the monotonic relationship

significantly differed from one species to another. So, to increase the sample size would allow us to confirm or infirm our results with better confidence.
Our non-significant results may also, quite simply, say that group size has no effect on DTD. A possible hypothesis is the reduction in the number of antelopes in the Khutse Game Reserve (DWNP, 2018). This reduction could therefore lead to a reduction in competition and therefore a reduced need for movement to find the quantity of food required to feed an entire group. This phenomenon is known as density-dependent regulation, where factors such as food availability, territory, and breeding opportunities are influenced by the size of the population (Sibly and Hone, 2002). But to test this hypothesis, we would need a much larger dataset than we currently have.

Other factors that we tested separately for their impact on DTD are the sexual composition of the group (all males, all females or mixed) and the group social structure (family or all adults). In several studies on different species (herbivores and monkeys) , it has been shown that there are differences in movements between males and females and if there are juveniles or not (Debeffe et al., 2019; Ruckstuhl and Festa-Bianchet, 2010; Shimooka, 2005). We hypothesized that males would tend to move more than females to protect their territory. We also thought that groups where juveniles or subadults were present would walk shorter distances. In both cases, our results didn't evidence such impacts. It is likely that if there is an effect of these factors, it is not strong enough to be detected with our limited dataset. It would also have been interesting to see if there is a difference in the DTD estimates between bachelor males (who may move more because looking for females) and dominant males (already having a harem).
As in the case of the effect of group size on DTD estimates, to verify this we would need a lot of data.

Another factor that could have an impact on the DTD estimate is the season itself. We carried out our surveys during the dry season, with average day temperatures between 20 and 25°C, cold nights and little or no rain. During the wet season, however, daytime temperatures are much higher and rainfall is abundant. The body size of the target species influences thermal sensitivity, with larger animals having a lower surface-to-volume ratio than smaller animals and therefore a reduced heat dissipation capacity (Shrestha et al, 2014). One hypothesis could therefore be that the larger animals move less and less as temperatures rise again (i.e. during the wet season). Another hypothesis is that during the dry season, with the lack of water and food, animals have to move more to find the resources they need to survive (Berry et al, 2023). It would have been very interesting to see if there

was a significant difference between the average DTD estimates during the dry season and the wet season. If there is one, depending on the period during which the track survey is to be carried out, the corresponding seasonal empirical average DTD estimate should be used in the FMP, which would make it possible to obtain a more accurate density estimate. If the difference is not significant, we could perhaps combine the data from the two seasons to obtain a more precise average DTD estimate, covering a full year.

We did not have the opportunity to continue the study throughout the year. However, we could test if during the first half of the dry season (here from May to August) the DTDs had decreased or increased.

Our analyses did not show any significant results, except for the ostriches. For this species, the results should be treated with caution, as they are based on only five trailings. For these animals, their DTD increased throughout the dry season. To verify this trend, more successful trailings are needed and an attempt should be made at defining the reason why they move (e.g. to find food, to go from waterhole to waterhole, etc.).

For the other species studied, it is possible that during the three months spent in the Khutse reserve, the changes in the environmental conditions was not sufficient (e.g. resources abundant enough to feed everyone and therefore not requiring more movements) to cause a change in the DTD. More data is therefore needed to check whether a trend is emerging.

In the case of the various conditions (in this case group size, sex, social structure or advancement in the dry season) that can impact the DTDs of the species studied, obtaining larger sample sizes could ultimately be beneficial for the use of the FMP formula. Knowing whether there is a possible impact on DTDs would enable us to determine whether it would be interesting to have several estimates for $\hat{M}$ for the same species, with each estimate corresponding to a different situation (e.g. one estimate for large groups and another for small groups, etc.). Consequently, we could adapt the $\hat{M}$ parameter according to the conditions present during the track surveys. This would give more accurate population densities, if there is indeed an impact of these variables on the DTDs.

In conclusion, this study enabled us to obtain more accurate empirical average DTD estimates for five herbivore species. These results have also enabled us to create a correction coefficient for the Kalahari populations that we can apply to the allometric average DTD estimates directly, in cases the target species does not have an empirical average DTD estimate. Our findings will potentially

contribute to the refinement of the track survey methodology ; in our case, the refinement of the $\hat{M}$ parameter in the FMP formula and therefore of the population density estimate obtained.

Another important aspect of this study is the involvement of local community members in research and conservation programs. Indeed, without the skills of the trackers, it would have been impossible to obtain such accurate DTDs in the field. This is further proof of the importance of preserving their knowledge.

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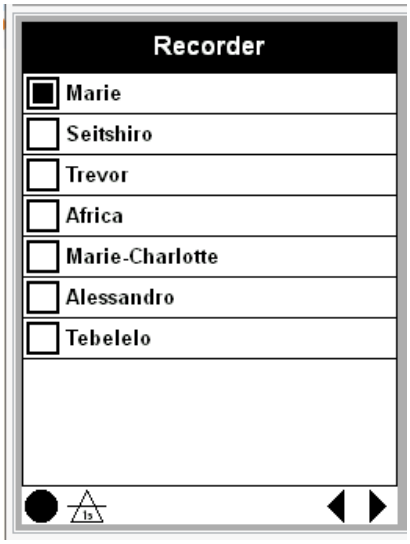
# VI. Appendice

## Appendix 1 : Use of the CyberTracker application

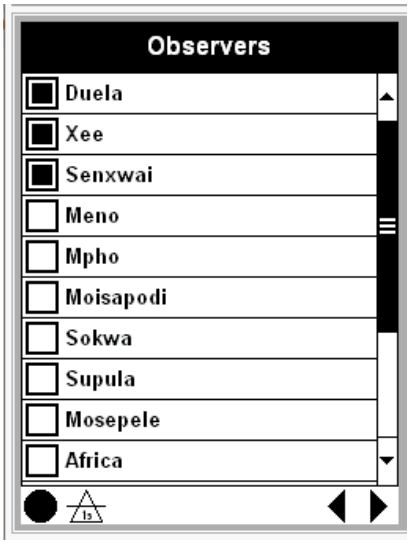
The Cybertracker app used to collect the data during fieldwork has been developed specifically for this project by Gielen, M-C. and Araldi, A. in 2023.

Day 1 : recording a spotting of a group of six greater kudus composed of four adult females and two subadult males.


Step 1 : application introduction page



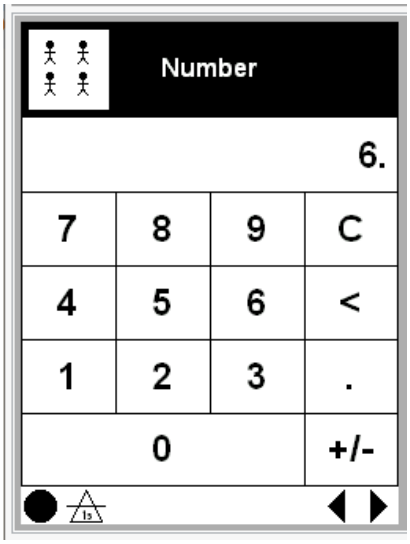

Step 2 : choice of the recorder



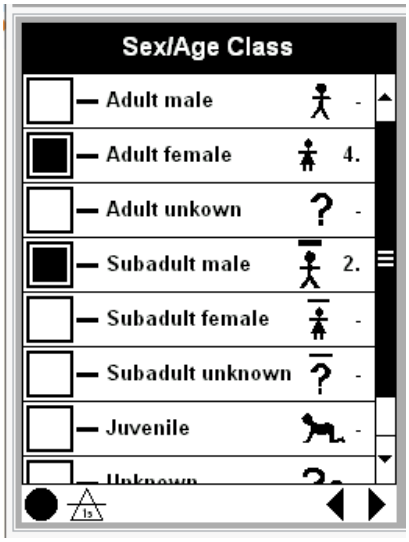

Step 3 : choice of the observers


Step 4 : choice of the tracking activity

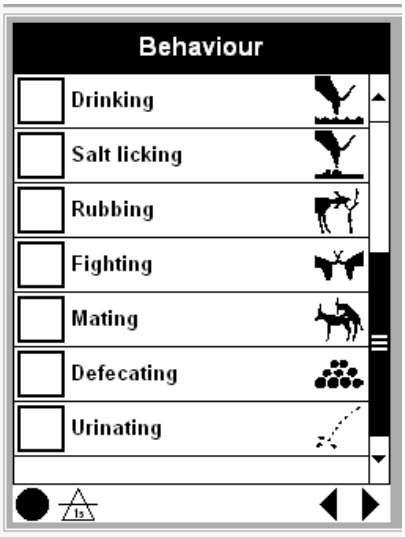

Step 5 : choice of the species of the spotting




Step 6 : information on the number of individuals



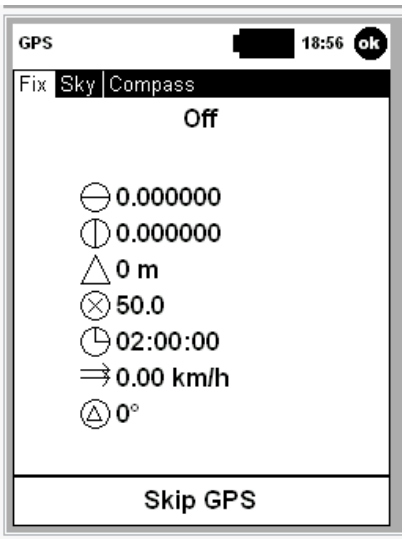

Step 7 : information on the sex of individuals and their number by sex


Step 8 : information about their behaviour at the time we saw them


Step 9 : photo of our animals

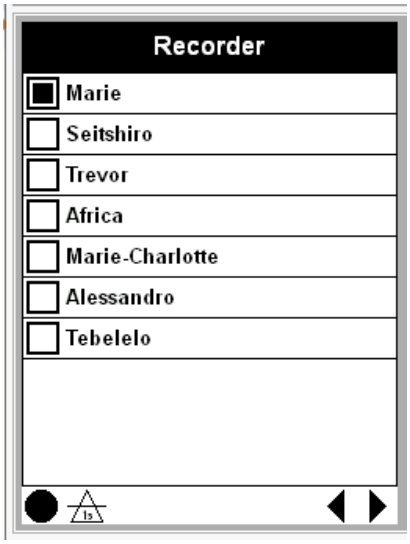

Step 10 : Note if important detail to report



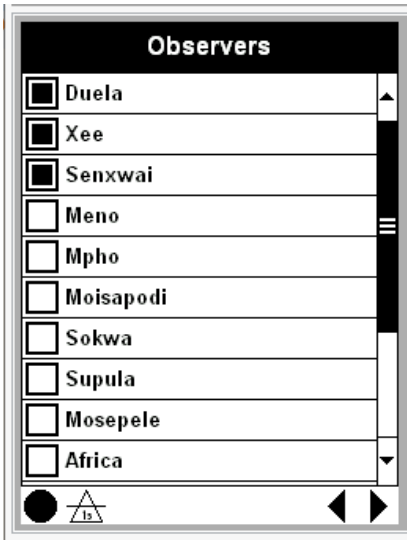

Step 11 : spotting recording

Day 2 : recording the trailing of a group of six greater kudus composed of four adult females and two subadult males.


Step 1 : application introduction page



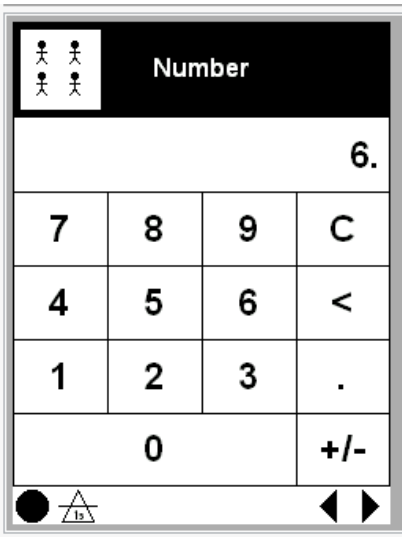

Step 2 : choice of the recorder



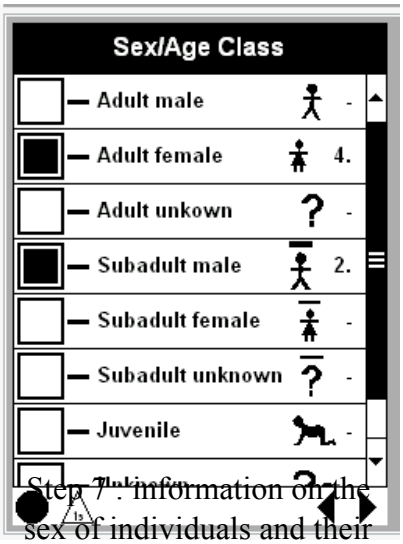

Step 3 : choice of the observers


Step 4 : choice of the tracking activity

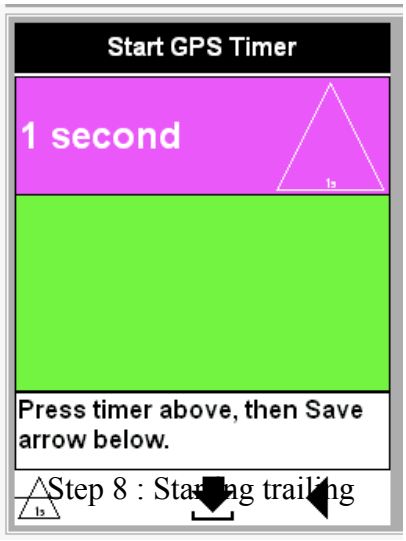

Step 5 : choice of the species of the trailing



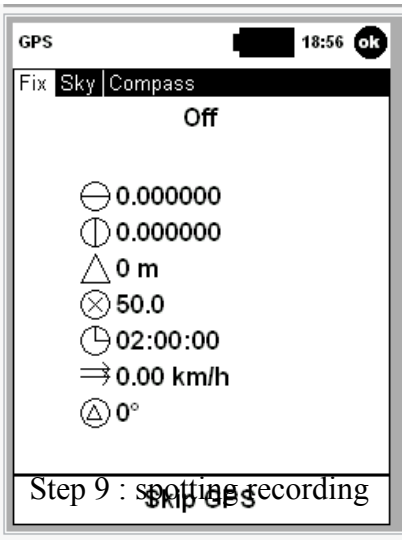

Step 6 : information on the number of individuals




Step 7 : information on the sex of individuals and their number by sex

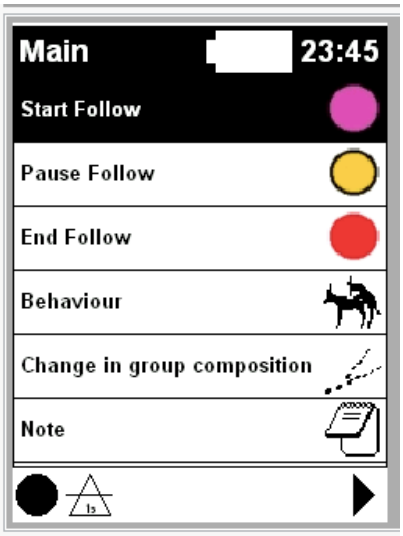



Step 8 : Starting trailing

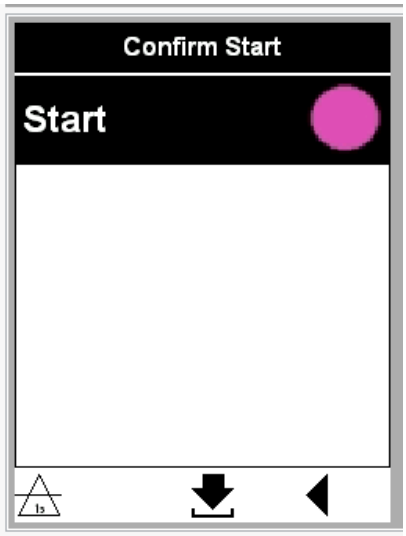



Step 9 : spotting recording

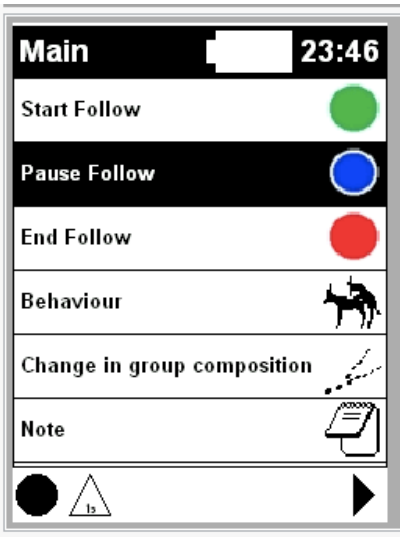
Once this information has been recorded, we can start the trailing :



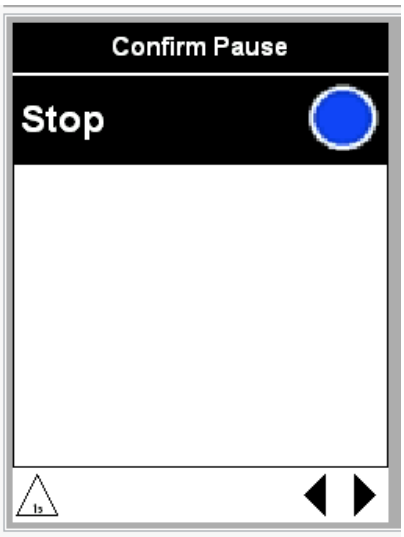

Step 10 : useful parameters during the trailing, here « Start Follow »




Step 11 : activation of trailing registration

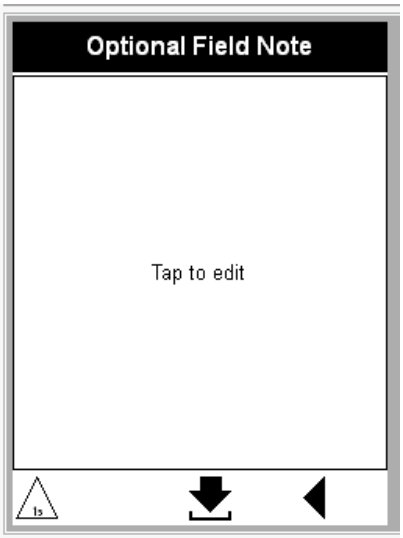



Step 12 : useful parameters during the trailing, here « Pause Follow »



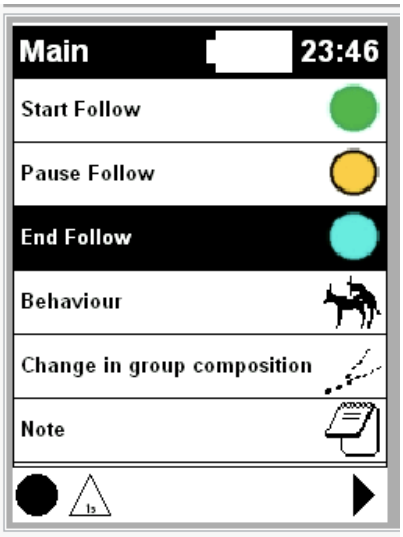

Step 13 : pausing trailing recording


Step 14 : reason for the break

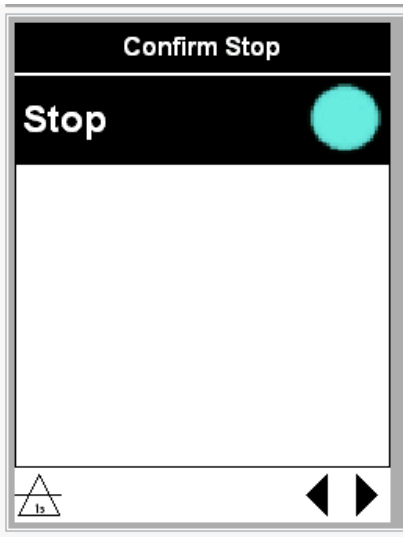



Step 15 : Note if important detail to report

To reactivate trailing edge recording, repeat steps 10 and 11.

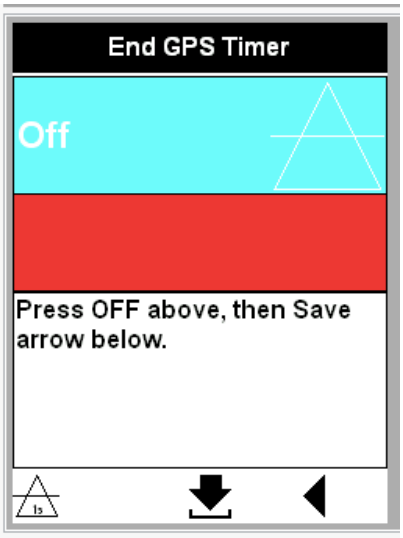



Step 16 : useful parameters during the trailing, here « End Follow »

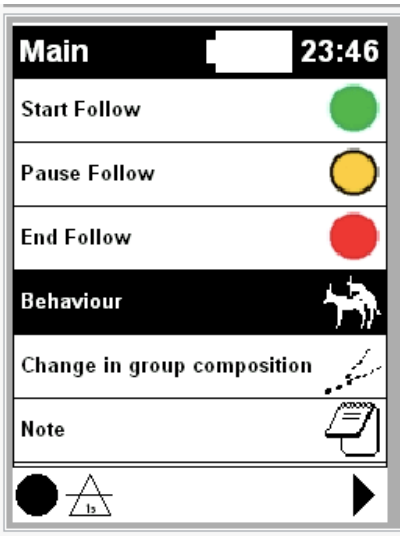



Step 17 : confirmation that trailing has come to a complete stop

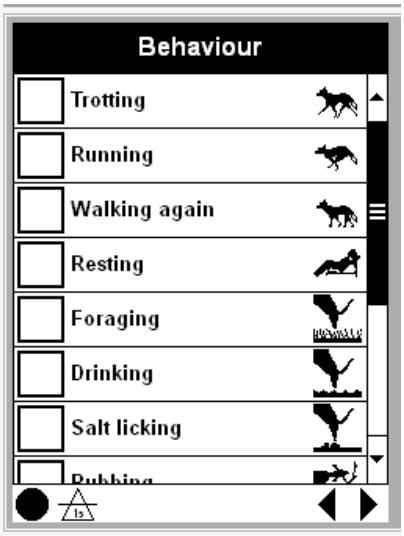

Step 18 : reason for spotting the trailing

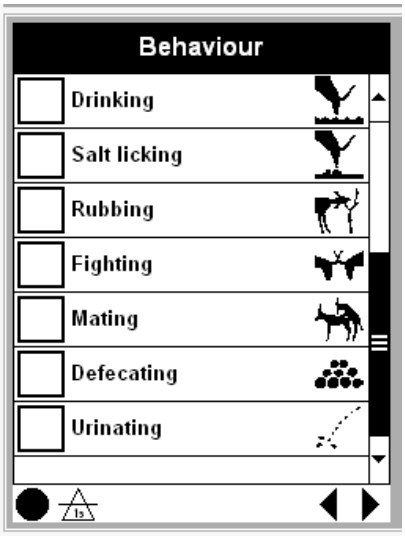



Step 19 : complete trailing stop

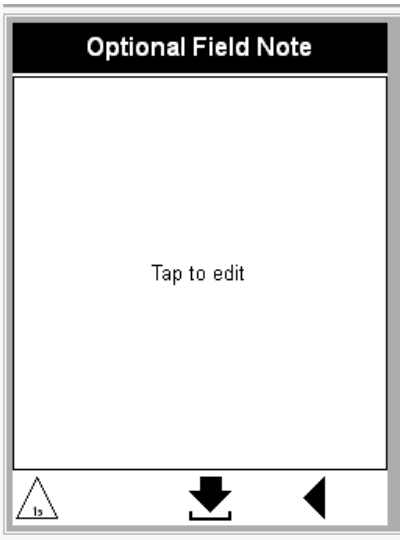



Step 20 : useful parameters during the trailing, here « Behaviour »

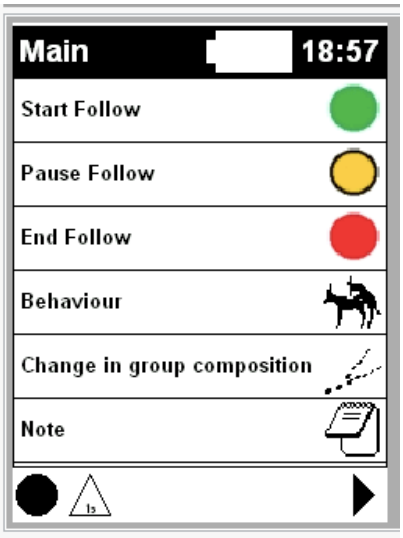


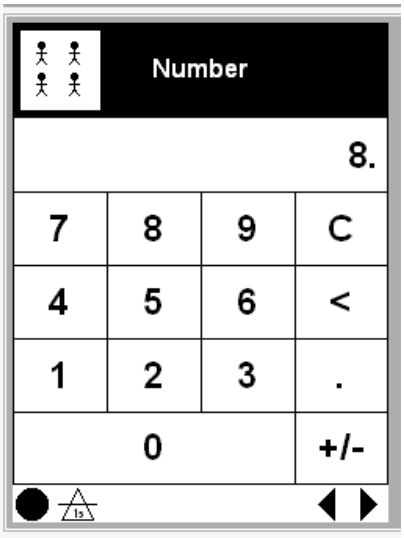

Step 21 : Choice of the behaviour



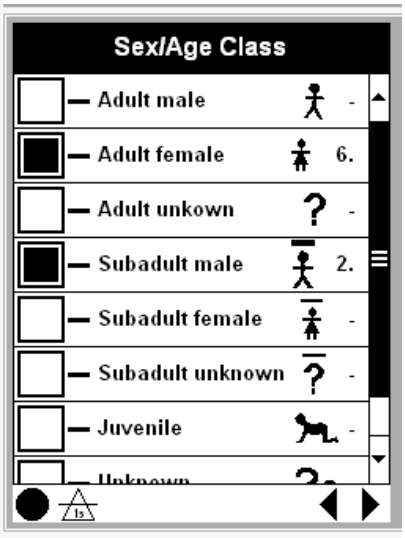

Step 22 : Note if important detail to report



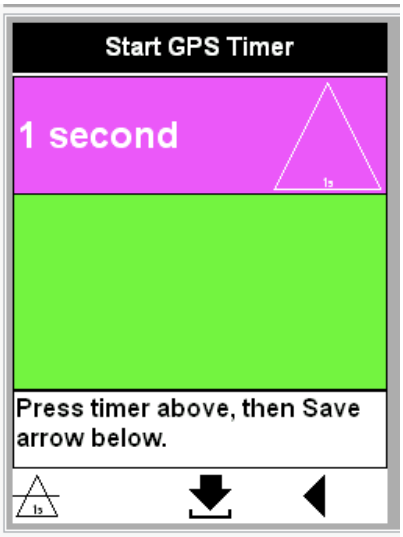

Step 23 : useful parameters during the trailing, here « Change in group composition »




Step 24 : new number of individuals in the group




Step 25 : information on the sex of individuals and their number by sex




Step 26 : confirmation of the change in the composition of the group

## Appendix 2 : Detailed field protocol

The field protocol has been developed specifically for this project by Gielen, M-C. and Araldi, A. in 2023 with the fundamental technical support of DR. Keeping and LEC tracking team.

Field team : 2 recorders, 3 observers, 1 driver (knowing that the driver could be one of the 2 recorders or one of the trackers who also had this qualification) with a car.

Among our five target species, the field protocols for springboks and ostriches were slightly different, so they will be detailed separately.

Day 1 : the spotting

The long-follow method involves spotting an individual or a group of individuals.
To do this, the team (with one member on the roof of the car to optimise our chances of animal detection), travelled the roads of the reserve to find one of the target species. When a group of individuals was spotted (here we'll be focusing on elands, greater kudus or red hartebeests), we stopped far enough away from them not to disturb them.
We then recorded the following information:

- Note the time we first saw them.
- Take a photo of the individual or group of individuals. We needed a zoom, to see the individuals and therefore have a better chance of not getting the wrong group for the next day's trailing. And a panorama, to make it easier to find the exact location where the individual or individuals were seen during the spotting.
- Record all the necessary information on the CyberTracker application (Appendix 1) : the recorder, the observers, the tracking activity, the species followed, the number of individuals, the sex (male, female or unknown), the age (adult, subadult, juvenile or unknown), the behaviour when we saw them, and a picture.
- Mark the location on the GPSMAP64s to have a backup of the spotting coordinates.

If we had time and were sure that our presence would not disturb the animals, we could stay and continue to observe them. This technique gives us a bigger window of opportunity for the next day's trailing. For example, if we carry out a spotting at 11:30am, observe the animals for 30 minutes and they remain in the same place during this time. The next day, it means we can complete the trailing between 11:30am and 12:00 without bias.

Once all the necessary information had been noted down, we could leave (always making sure not to disturb them).

In the case of elands, greater kudus and red hartebeests, we couldn't spot before 11am, otherwise we wouldn't have had enough time the next day to finish trailing. To start trailing, we needed daylight. From May to August, the sun rose at around 7am so we couldn't start before then. In addition, to have a better chance of finishing the trailing, we needed at least 4 hours to complete it. So 11am was the earliest we could start spotting.

For the springboks, time was not an issue. These animals almost always stayed in the same place, in a pan. So we were almost certain to find them in the same pan the next day. Therefore, we could spot this species at any time of day, such as we could see them and record their location at the time the 24h would have elapsed.
Once a group of springbok had been spotted by the team, we repeated the same steps as for the elands, greater kudus and red hartebeests.

Ostriches were particularly difficult to track. In fact, when these animals walk on harder ground, as they do on pans, their footprints are virtually unprinted, so all you can see is the trace of their claw (a small hole). So, to maximise our chances of success for the trailing, the spotting adhered to additional criteria. We only spotted ostriches if they were in a group (a strict minimum of two). Spotting had to take place as late as possible in the day to give us as much time as possible the next day. We were not to spot ostriches in a pan. As the ground was too hard, their footprints wouldn't imprint on the substrate and we couldn't follow the trail.
If the spotting met all these criteria, we repeated the same steps as for the species seen previously.

Over the course of a day, several spottings (different groups, species or locations) were carried out to the extent possible.
The aim of this manoeuvre was first to enable us to choose the best option for the next day's trailing. We chose according to the species we already had data for, the place where the spotting took place, the size of the group, and so on.
The second objective was to have back-ups in case the next day's trailing didn’t go as expected (trail lost, animal killed, etc.). Depending on the time we had left, we could start another trailing session to avoid losing a day's work.

Day 2 : the trailing

The next day, the team would return to the exact spot where the individual or group of individuals had been spotted. For elands, greater kudus and red hartebeests, we could return 4 or 5 hours before the time at which the spotting was recorded. For ostriches, we had to return 7 to 8 hours before the spotting time.
For the springboks we arrived 15 minutes before spotting time. The springboks were always around the same place where we had spotted them the day before. So, once the spotting time had arrived, with the GPS, we went to the place where they were at the end of the 24 hours to mark the spot. Then we did the trailing just like the others, except that we knew exactly where the trailing would end up.

Once at the start point of the trailing, the team got into place. Two of the trackers led the way, with one of the recorders following. The last tracker followed us in the car with the second recorder on the roof. The second recorder could check whether we were close to the animals we were tracking, warn us if he saw any interesting spotting for the next day or alert us to any potential danger.
To start trailing, we had to be at the exact spot where the animals had been seen (by checking the coordinates but also the photos taken the day before). Once there, we could activate the CyberTracker application by specifying certain information (Appendix 1) : the recorders, the observers, the tracking activity, the species followed, the number of individuals, the sex, the age and start the GPS timer. We also marked our starting location on the handheld GPS, which also recorded our movements. This allowed us to have a back-up in case the CyberTracker application and/or the smartphone stopped working. Once the coordinates had been recorded, we could start trailing by pressing the 'Start Follow' button on the CyberTracker application. The trackers then showed the path taken by the animals. To be as accurate as possible, the recorder had to walk as much as possible in the animal tracks shown by the trackers.

During trailing, a number of things could happen. These events might require you to pause the CyberTracker application using the « Pause Follow » button :

- In the event that the trackers need to search for tracks and signs of the tracked individual(s) followed. In this situation, the recorder stays at the place where the last track was seen. Then,

once the trackers had found the trail again, the recorder could press the "Start Follow" button to indicate the trailing was resumed.

- If the animal was seen during the trailing, the team stopped and made as little noise as possible. In this situation there were 2 possibilities. The first was that we saw our animal but it didn't see us, so we tried to hide (by sitting in the bush, etc.) so as not to influence the animal's behaviour. Then we waited, and either he left after a while and we could continue trailing. Or we waited until spotting time. Once it was past spotting time, you could move towards the animal and record exactly where it was standing at spotting time. The second possibility was that the animal saw us and ran away because of us. In this situation, we had to stop for at least an hour to allow the animal to calm down and resume its activities, so that we could continue trailing (by reactivating the CyberTracker application by pressing "Start Follow").

There could also be other reasons for requesting a break, such as to make repairs to the car, for the team to rest, or to signal a danger.
Once the break was over, we had to press the button « start » on the CyberTracker application again.

Trackers could also give us information on the behaviour(s) that our individual(s) have adopted : trotting, running, walking again, resting, foraging, drinking, salt licking, rubbing, fighting, mating, defecating and urinating (Appendix 1). Additionnally, the trackers gave us an estimate of the time at which the animal performed the behaviour.

Sometimes, during trailing, the composition of the group we were following changed. In this case, thanks to the "Change in group composition" button on the CyberTracker application, we could redefine the number of individuals, sex and age and then continue trailing by pressing "Start Follow ».

Once we had managed to complete the 24 hours of trailing, i.e. we had seen the animal or found the place where it was resting or eating, or when trackers estimated the trail to be completed in case the animal was not seen on time and the trailing was pursued, we could stop the recording definitively. To do this, on CyberTracker, we pressed the "End Follow" button, selected the reason for stopping the trailing (trailing complete, trail lost, animal dead, breakdown, danger, field team member ill or other). Then we marked the location on the handheld GPS as "trail end ».

## Appendix 3 : Recorded trails

This table shows raw (uncorrected) data from trailings carried out during the three months of fieldwork (May 15 to August 15).

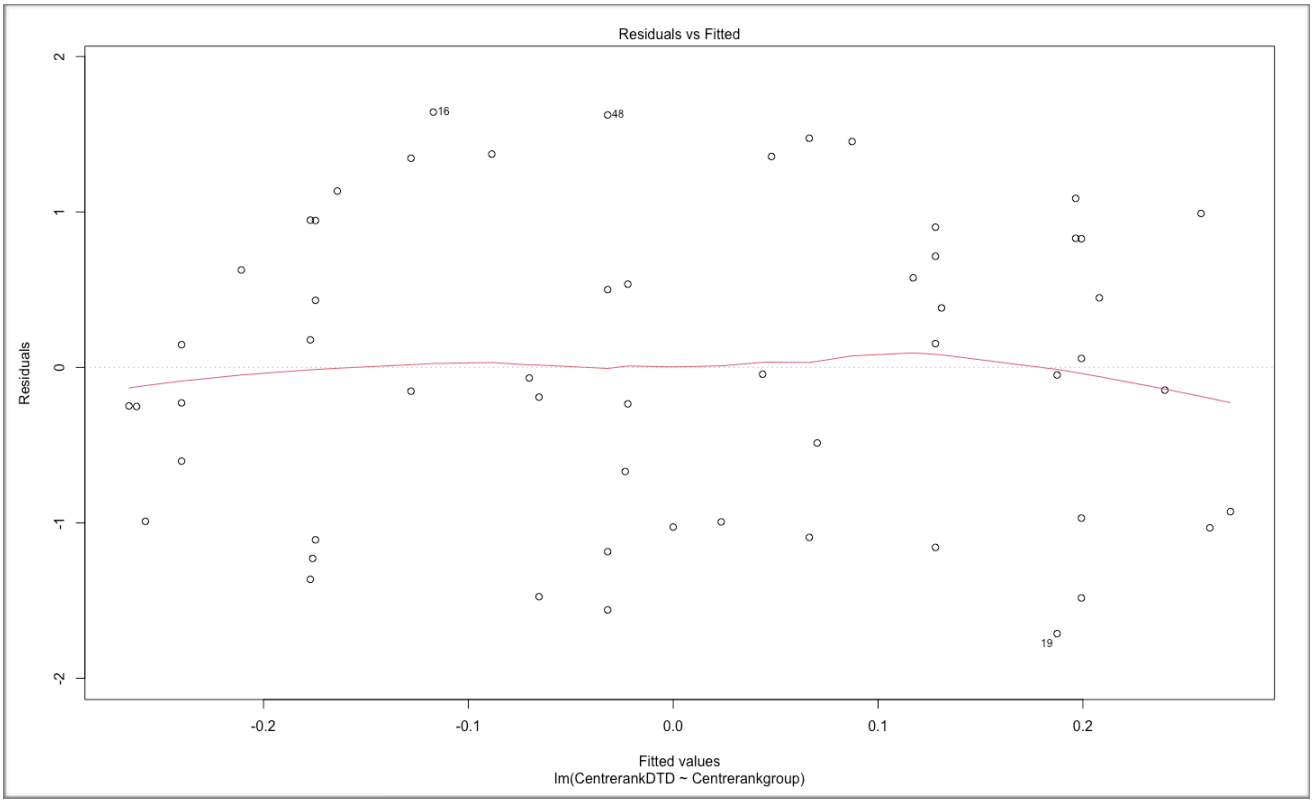
| Date | Species | Number of individuals followed | Trail completed | Animal seen at the end of the trailing | Trail length (km) | Number of hours completed |
|---|---|---|---|---|---|---|
| 16/05/2023 | Hartebeest | 12 | Yes | Yes | 3.217 | 24 |
| 17/05/2023 | Springbok | 35 | Yes | Yes | 2.411 | 24 |
| 18/05/2023 | Eland | 50+ | Yes | Yes | 10.673 | 24 |
| 19/05/2023 | Ostrich | 2 | Yes | No | 2.799 | 24 |
| 22/05/2023 | Springbok | 43 | Yes | Yes | 1.591 | 24 |
| 23/05/2023 | Hartebeest | 4 | Yes | No | 5.977 | 24 |
| 24/05/2023 | Kudu | 7 | Yes | Yes | 7.171 | 24 |
| 25/05/2023 | Kudu | 1-2 | Yes | No | 3.566 | 24 |
| 26/05/2023 | Hartebeest | 5 | Yes | No | 10.466 | 24 |
| 29/05/2023 | Ostrich | 2 | No | No | 3.050 | 23 |
| 30/05/2023 | Hartebeest | 1-10 | Yes | Yes | 11.162 | 24 |
| 31/05/2023 | Springbok | 26 | Yes | Yes | 2.903 | 24 |
| 01/06/2023 | Ostrich | 2 | Yes | No | 3.363 | 24 |
| 02/06/2023 | Hartebeest | 12 | Yes | Yes | 10.261 | 24 |
| 05/06/2023 | Ostrich | 8 | No | No | 1.933 | 2 |
| 05/06/2023 | Springbok | 40 | Yes | Yes | 2.306 | 24 |
| 06/06/2023 | Ostrich | 1 | No | No | 2.853 | 12 |
| 07/06/2023 | Ostrich | 1 | No | No | 3.396 | 20 |
| 08/06/2023 | Hartebeest | 7 | Yes | Yes | 6.266 | 24 |
| 09/06/2023 | Kudu | 3 | No | No | 1.299 | 1 |
| 09/06/2023 | Springbok | 4 | Yes | Yes | 2.023 | 24 |
| 12/06/2023 | Hartebeest | 12 | Yes | Yes | 1.881 | 24 |
| 13/06/2023 | Hartebeest | 4 | Yes | Yes | 9.026 | 24 |
| 14/06/2023 | Hartebeest | 7 | Yes | Yes | 4.774 | 24 |
| 15/06/2023 | Kudu | 3 | No | No | 0.299 | 4 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 15/06/2023 | Kudu | 1 | Yes | No | 4.390 | 24 |
| 19/06/2023 | Kudu | 10-4 | Yes | Yes | 6.867 | 24 |
| 20/06/2023 | Springbok | 4 | Yes | Yes | 1.145 | 24 |
| 21/06/2023 | Kudu | 3 | Yes | No | 8.177 | 24 |
| 21/06/2023 | Kudu | 6 | Yes | Yes | 6.639 | 24 |
| 22/06/2023 | Kudu | 12 | Yes | Yes | 4.815 | 24 |
| 23/06/2023 | Hartebeest | 2 | Yes | No | 4.646 | 24 |
| 26/06/2023 | Kudu | 1 | Yes | No | 5.780 | 24 |
| 27/06/2023 | Springbok | 4 | Yes | Yes | 1.812 | 24 |
| 28/06/2023 | Eland | 2-10 | Yes | Yes | 6.113 | 24 |
| 29/06/2023 | Hartebeest | 10 | Yes | Yes | 3.040 | 24 |
| 30/06/2023 | Ostrich | 3 | No | No | 8.217 | 19 |
| 04/07/2023 | Springbok | 7 | Yes | Yes | 1.654 | 24 |
| 05/07/2023 | Kudu | 4 | Yes | Yes | 2.815 | 24 |
| 06/07/2023 | Springbok | 17 | Yes | Yes | 1.704 | 24 |
| 06/07/2023 | Kudu | 3 | Yes | Yes | 1.504 | 24 |
| 07/07/2023 | Ostrich | 8 | Yes | Yes | 7.998 | 24 |
| 10/06/2023 | Springbok | 7 | Yes | Yes | 0.899 | 24 |
| 10/07/2023 | Hartebeest | 4 | Yes | Yes | 1.124 | 24 |
| 11/07/2023 | Eland | 5 | Yes | No | 19.832 | 24 |
| 12/07/2023 | Eland | 100+ | Yes | No | 17.188 | 24 |
| 12/07/2023 | Eland | 30 | No | No | 18.851 | 23 |
| 13/07/2023 | Hartebeest | 12 | Yes | Yes | 6.166 | 24 |
| 19/07/2023 | Kudu | 4 | Yes | Yes | 11.168 | 24 |
| 20/07/2023 | Springbok | 14 | Yes | Yes | 1.256 | 24 |
| 20/07/2023 | Springbok | 3 | Yes | Yes | 1.611 | 24 |
| 21/07/2023 | Eland | 20-30 | Yes | Yes | 12.890 | 24 |
| 24/07/2023 | Ostrich | 2 | Yes | No | 8.571 | 24 |
| 25/07/2023 | Eland | 50+ | Yes | Yes | 4.856 | 24 |
| 26/07/2023 | Ostrich | 2 | No | No | 5.361 | 20 |
| 26/07/2023 | Springbok | 33 | Yes | Yes | 1.962 | 24 |
| 27/07/2023 | Kudu | 4 | Yes | Yes | 6.911 | 24 |
| 29/07/2023 | Kudu | 3 | Yes | Yes | 5.581 | 24 |

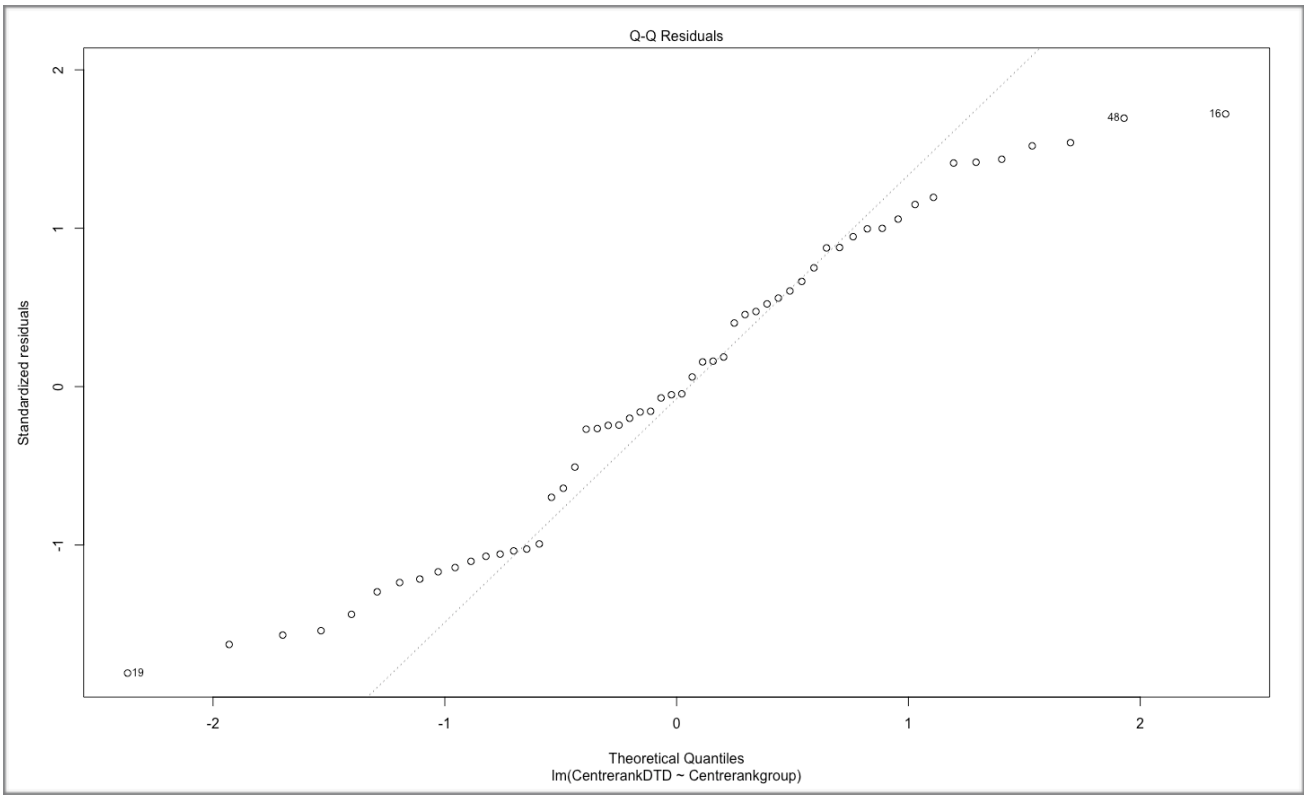
| | | | | | | |
|---|---|---|---|---|---|---|
| 31/07/2023 | Eland | 15 | Yes | Yes | 5.514 | 24 |
| 01/08/2023 | Eland | 17-30 | Yes | Yes | 8.298 | 24 |
| 02/08/2023 | Eland | 9 | Yes | Yes | 9.841 | 24 |
| 03/08/2023 | Eland | 3-30+ | Yes | No | 13.123 | 24 |
| 04/08/2023 | Kudu | 5 | Yes | Yes | 8.951 | 24 |
| 07/08/2023 | Kudu | 1-2 | Yes | Yes | 3.040 | 24 |
| 08/08/2023 | Eland | 2 | Yes | No | 13.415 | 24 |
| 09/08/2023 | Kudu | 6 | Yes | Yes | 7.364 | 24 |
| 10/08/2023 | Eland | 1 | Yes | Yes | 5.855 | 24 |
| 11/08/2023 | Kudu | 4 | Yes | Yes | 3.407 | 24 |
| 11/08/2023 | Eland | 9 | No | No | 14.144 | 9.5 |
| 14/08/2023 | Kudu | 6 | Yes | Yes | 7.419 | 24 |
| 15/08/2023 | Kudu | 6 | Yes | Yes | 3.720 | 24 |

(In green, we have the trailings for which the trails have been completed and the animals have been seen ; In orange, we have the trailings for which the trails have been completed but the animals have not been seen ; In red, we have the trailings for which the trails have not been completed and the animals have not been seen.)

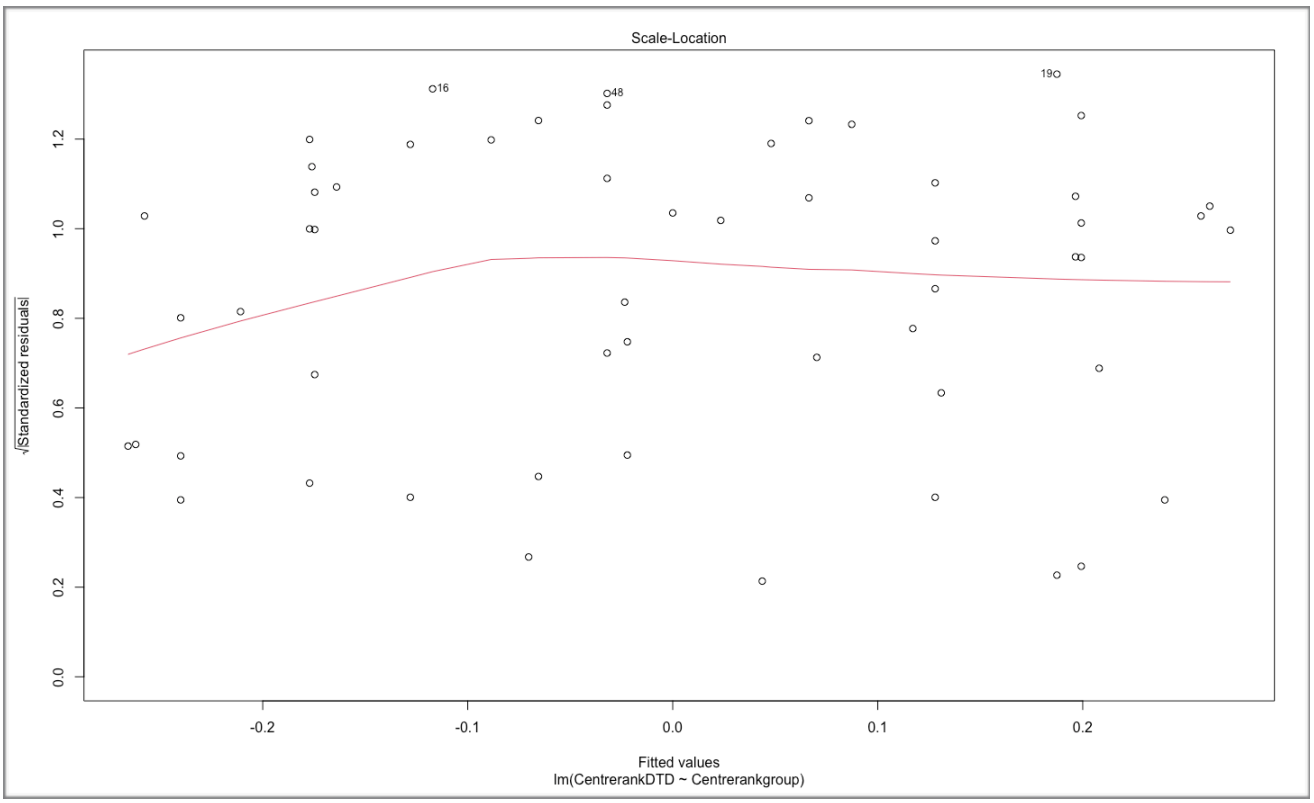
## Appendix 4 : Diagnostic plots for the effect of group size on average DTD estimate



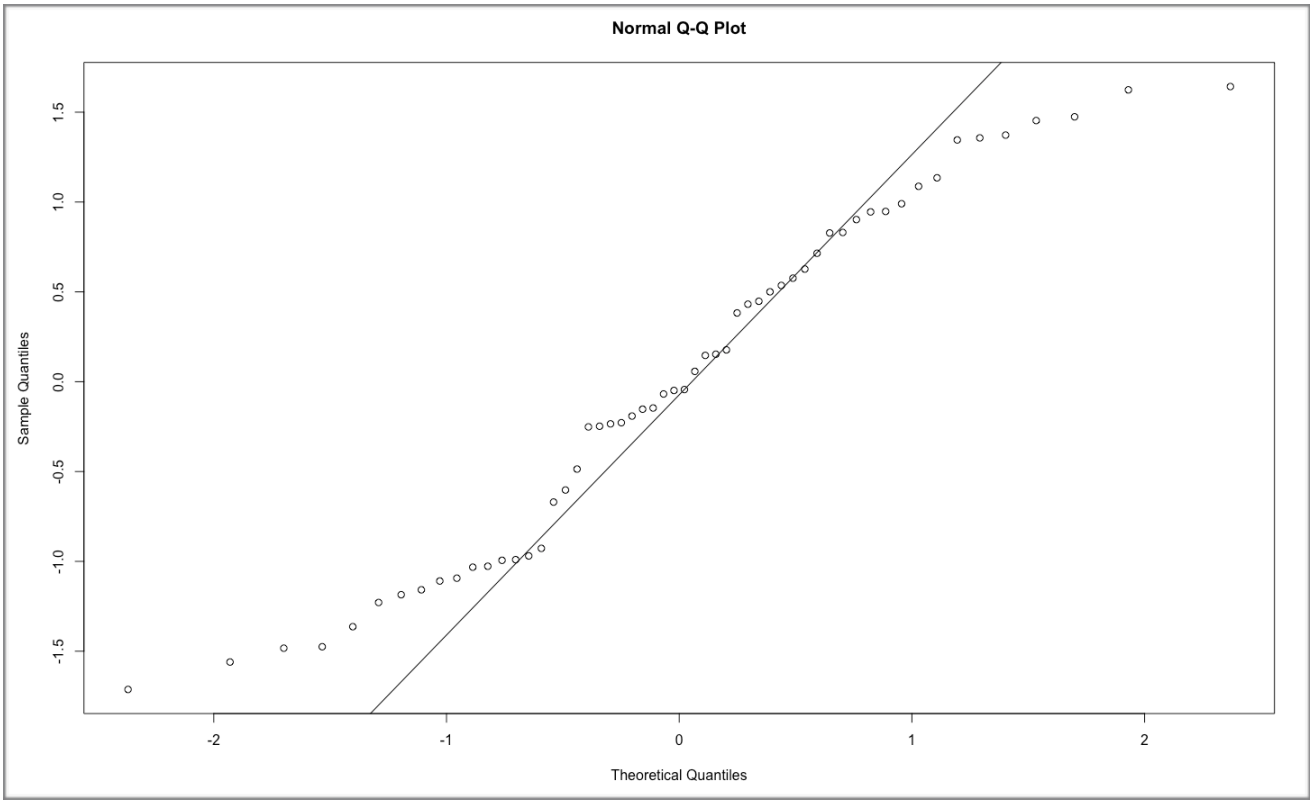

Plot to check linearity.




Plot to check the residuals.

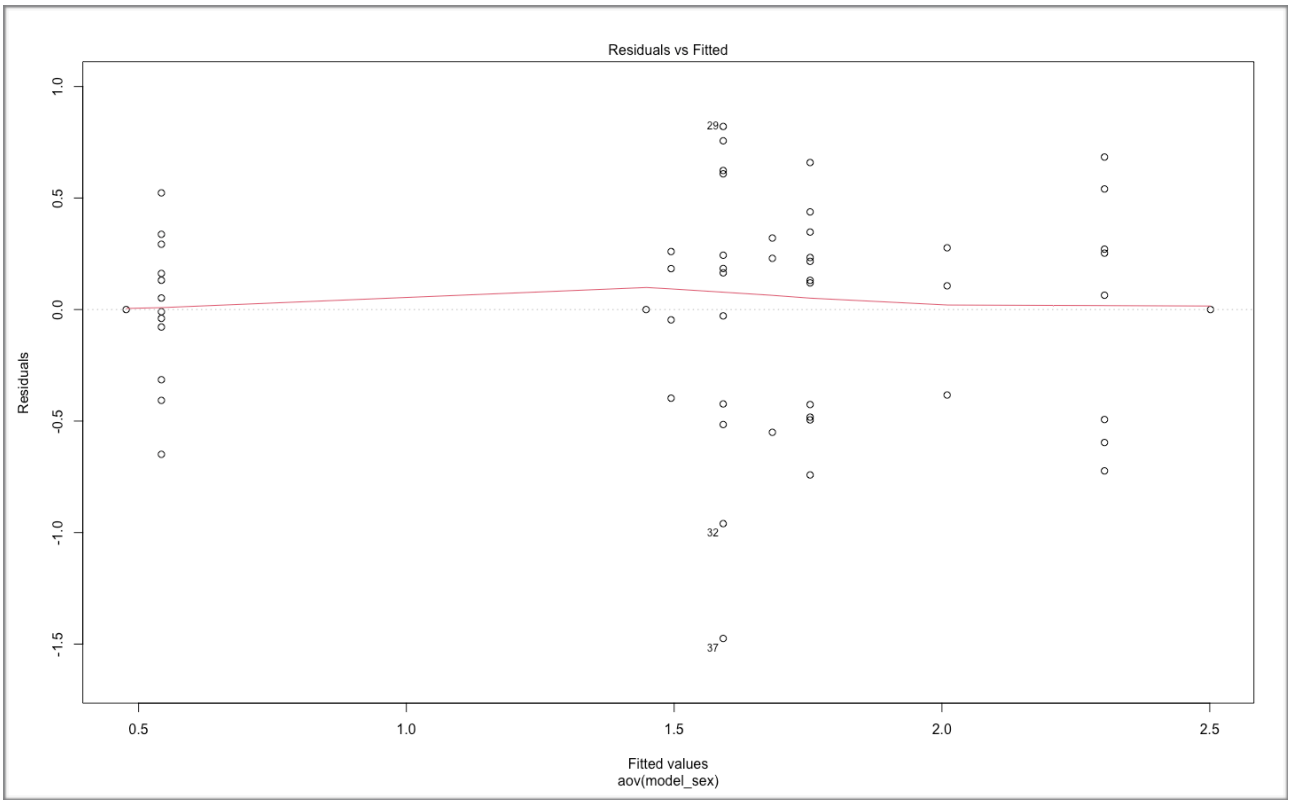



Plot to check homoscedasticity of errors.

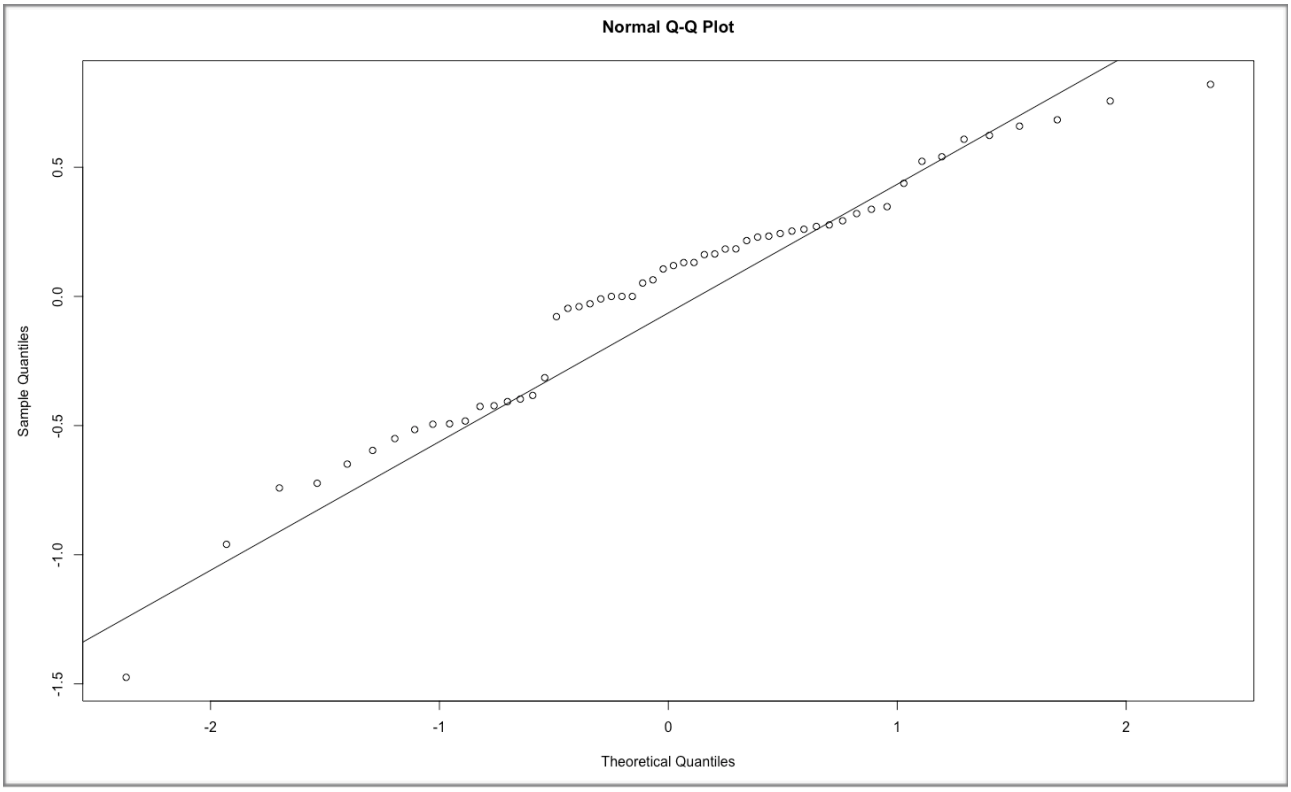



Plot to check normality of errors.

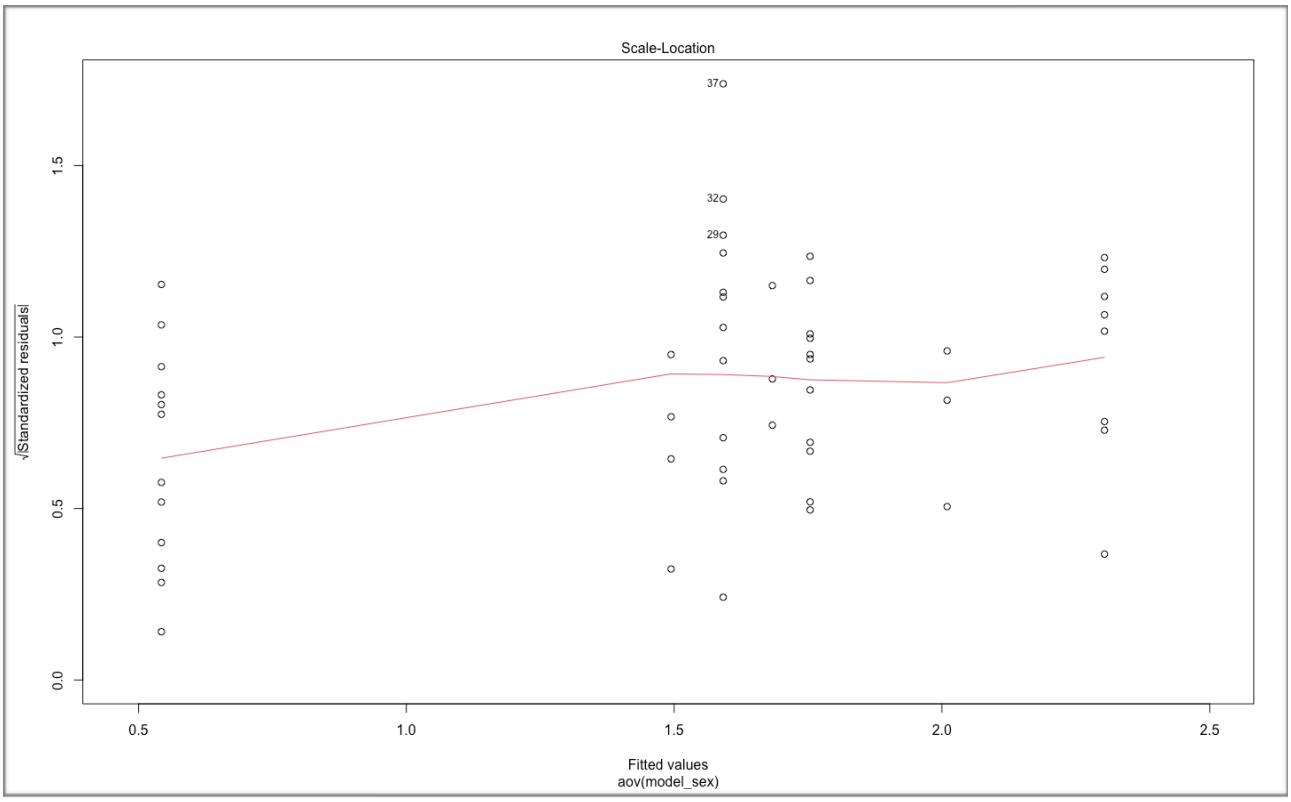
## Appendix 5 : Diagnostic plots for the effect of sex on average DTD estimate




Plot to check linearity.

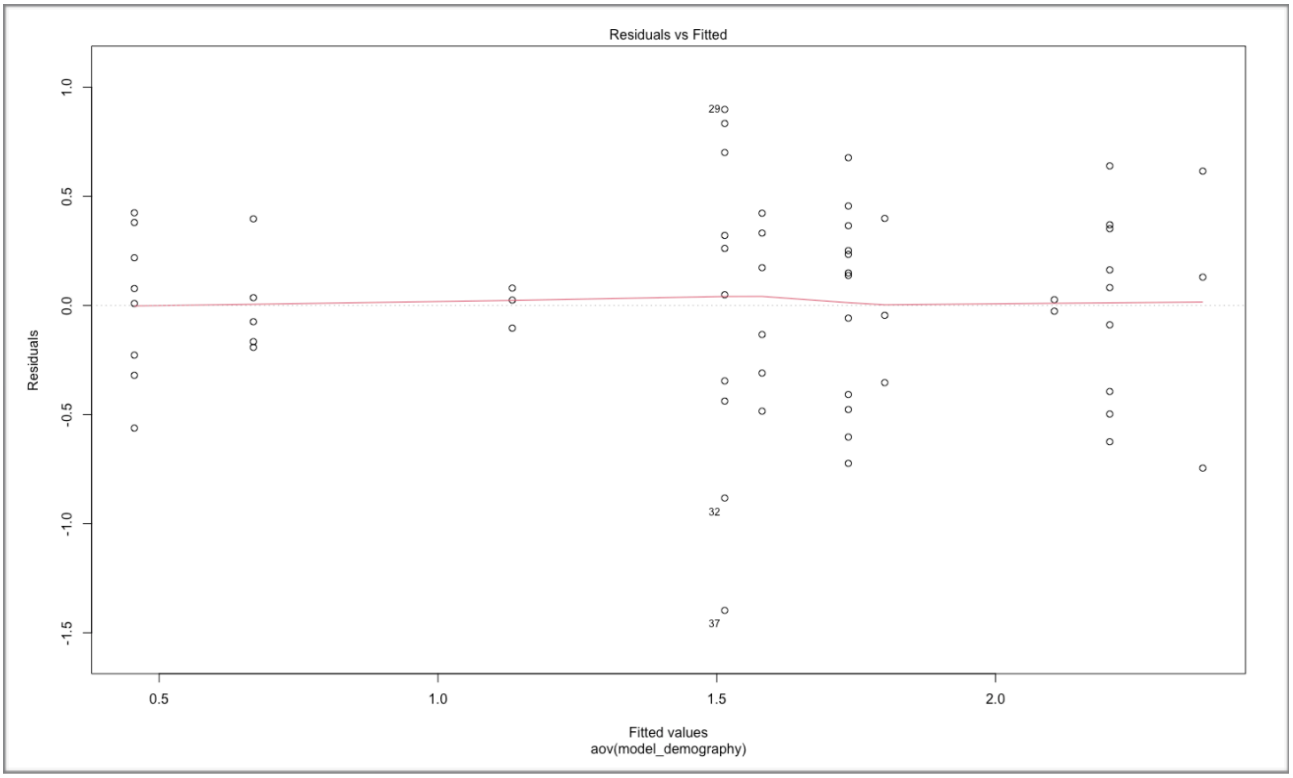



Plot to check the normality.

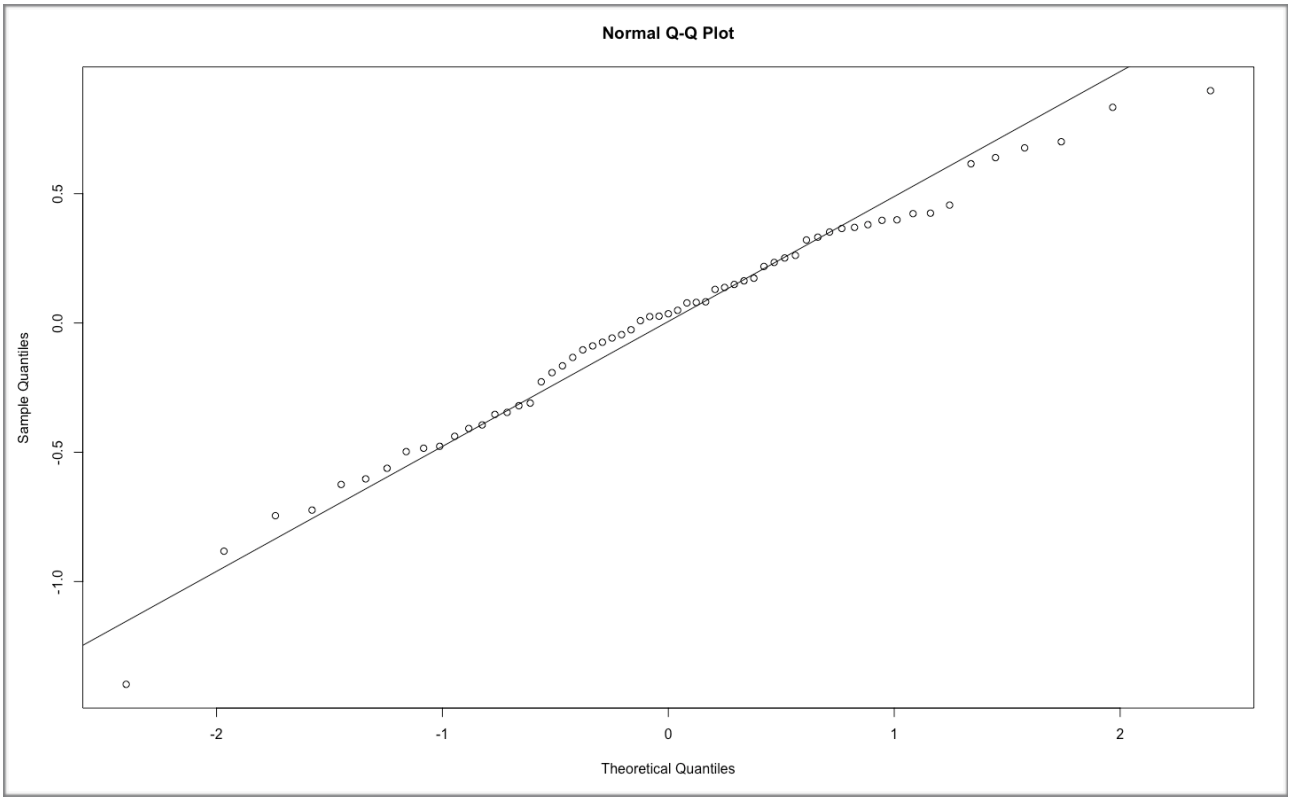



Plot to check homoscedasticity of errors.

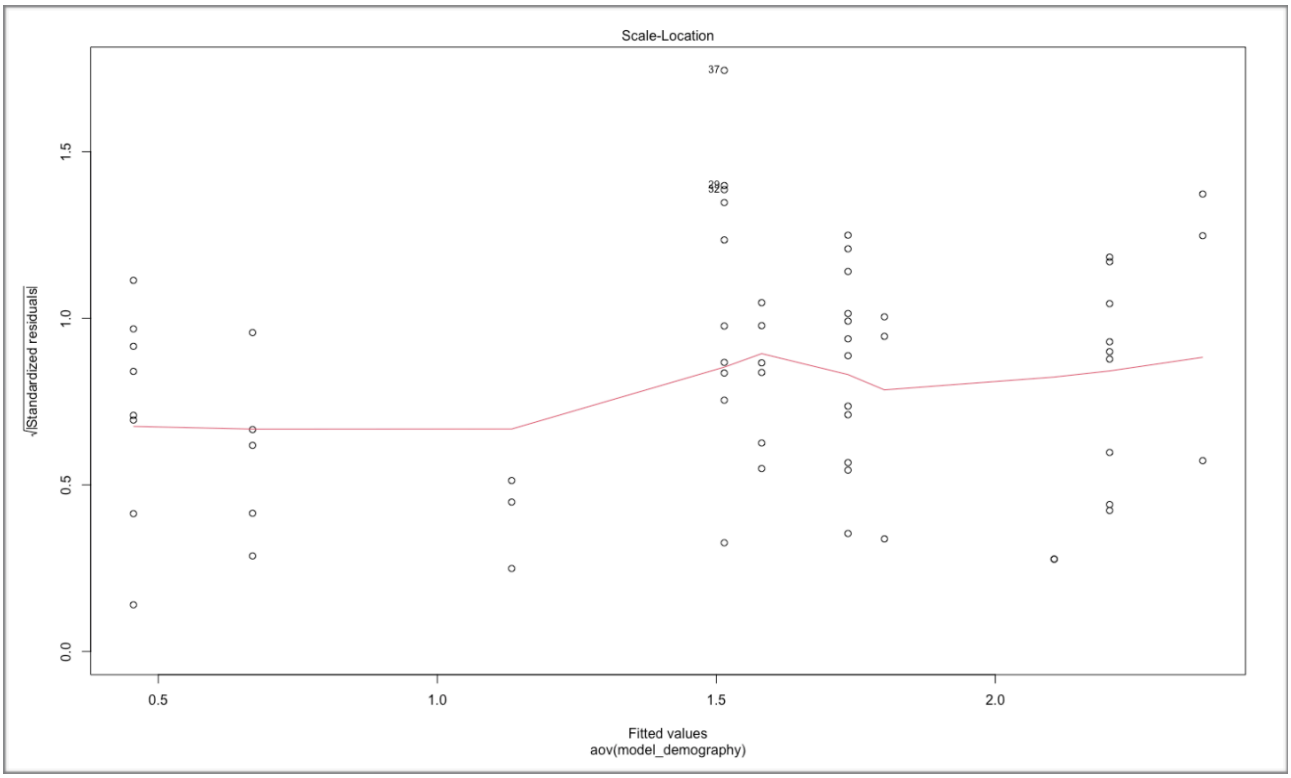
## Appendix 6 : Diagnostic plots for the effect of social structure on average DTD estimate




Plot to check the linearity.

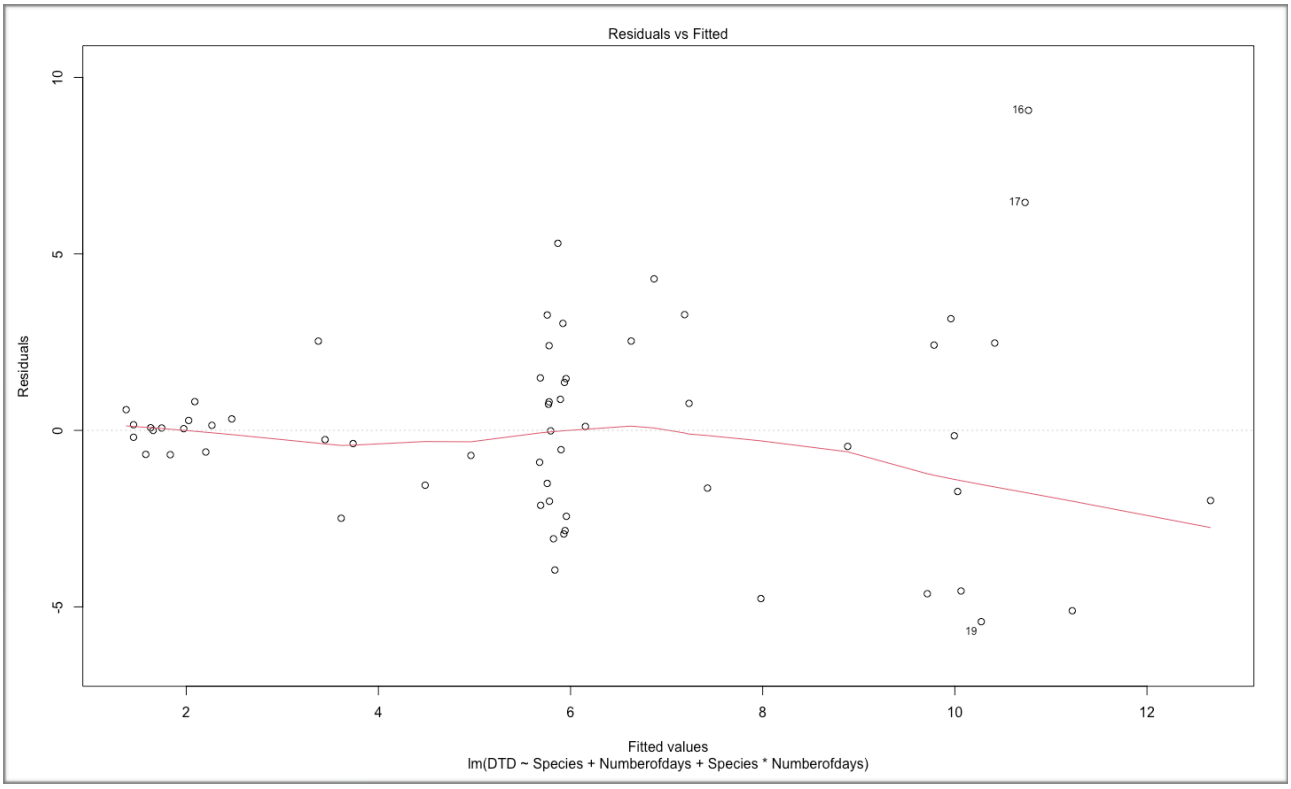



Plot to check the normality of errors.

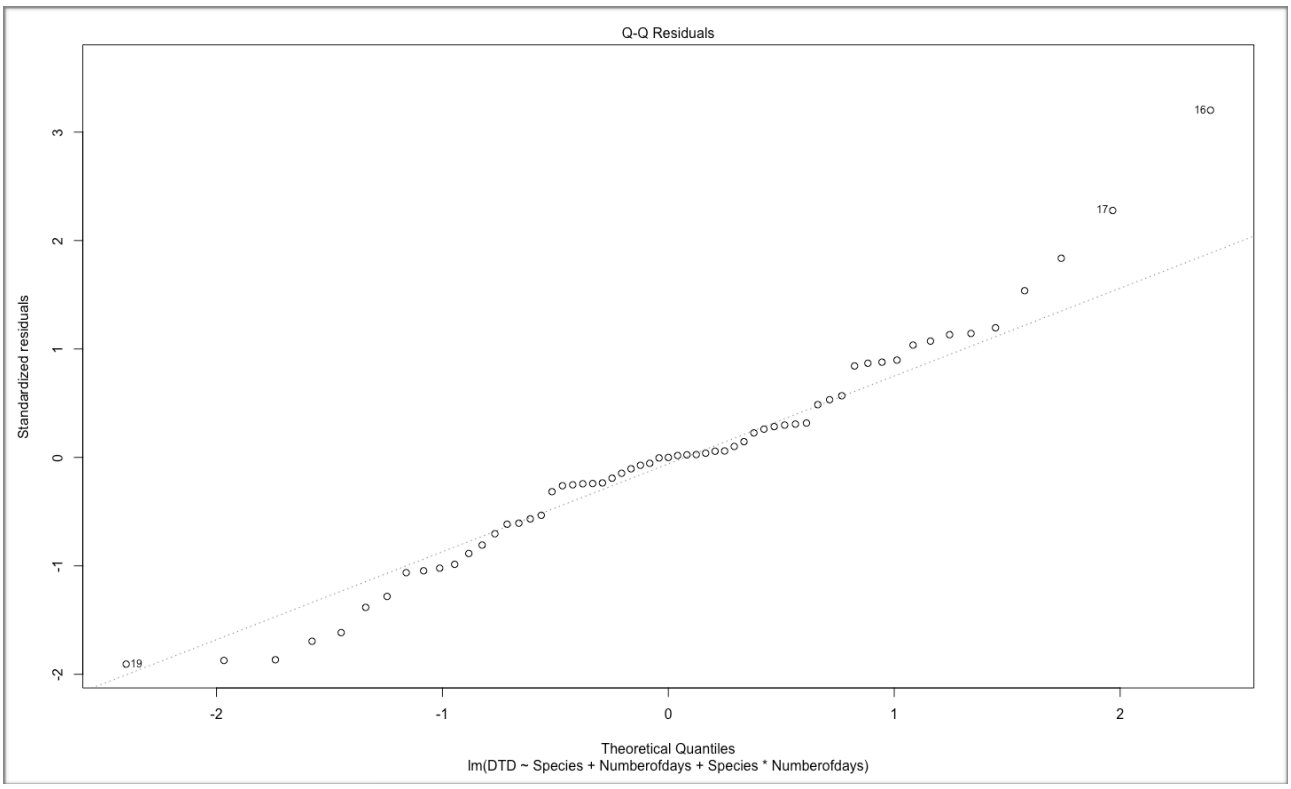



Plot to check homoscedasticity of errors.

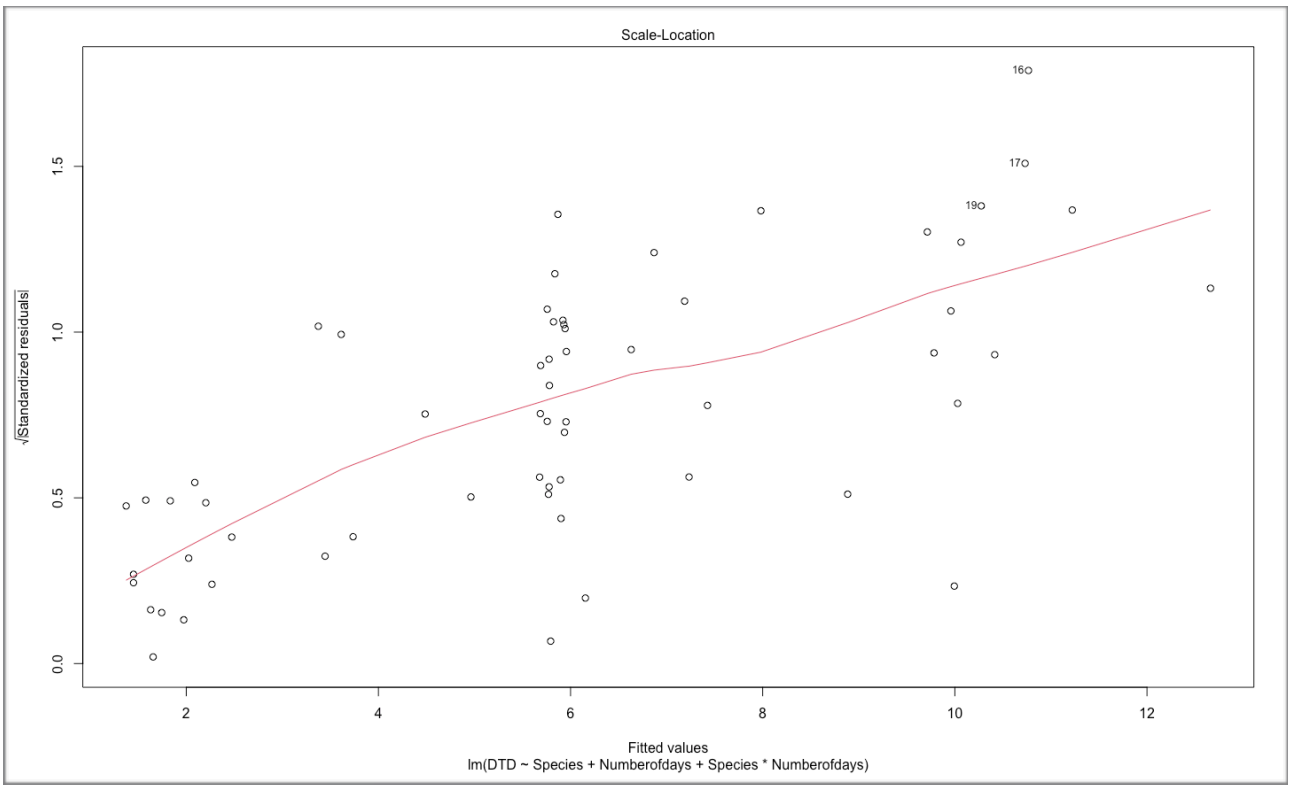
## Appendix 7 : Diagnostic plots for the effect of temporal progress in the dry season on average DTD estimate.



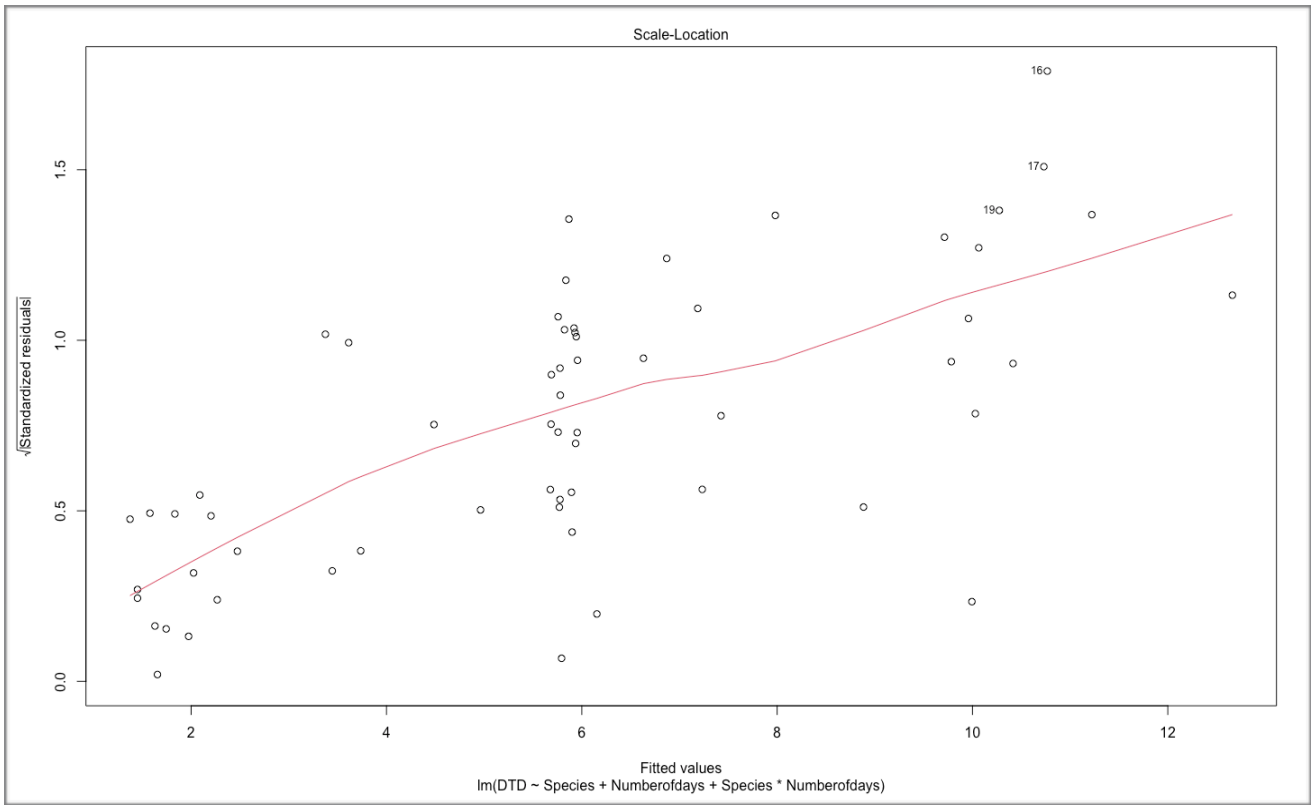

Plot to check linearity.




Plot to check the residuals.

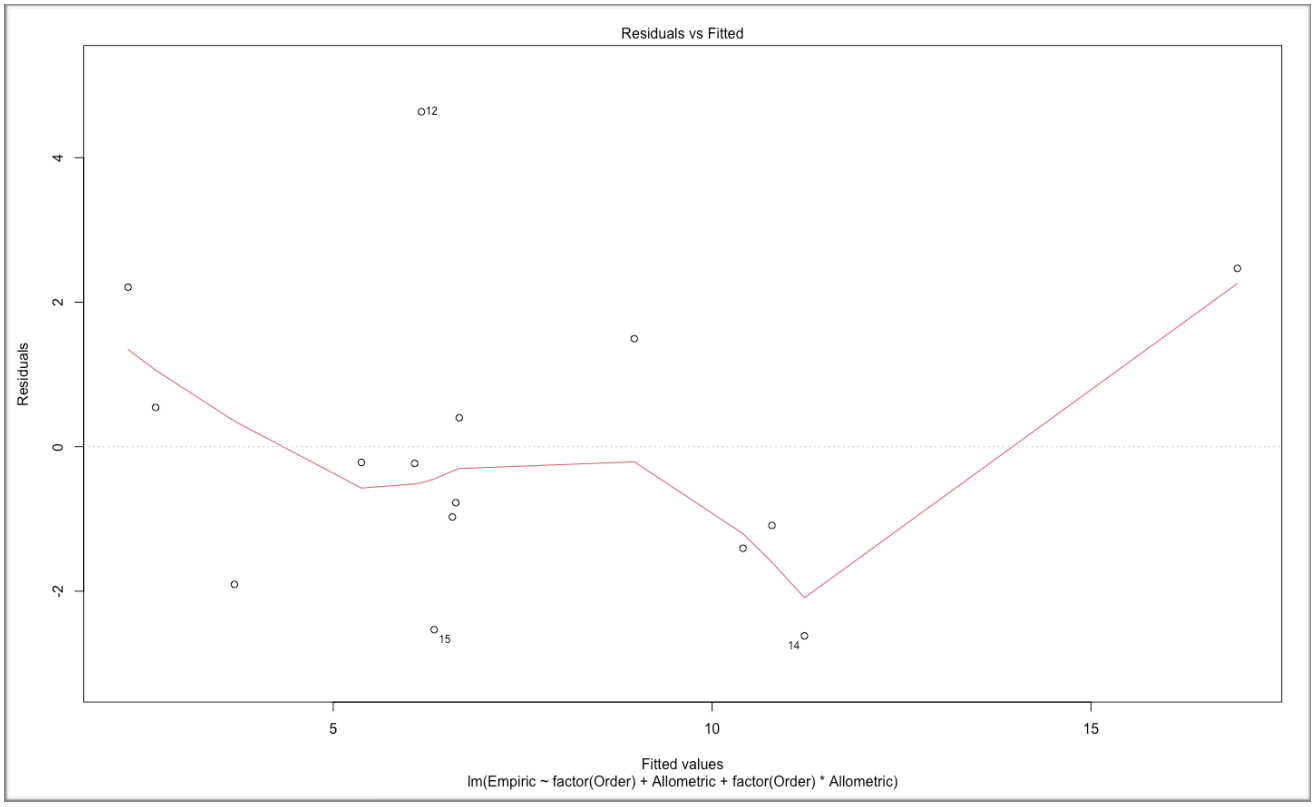



Plot to check homoscedasticity of errors.

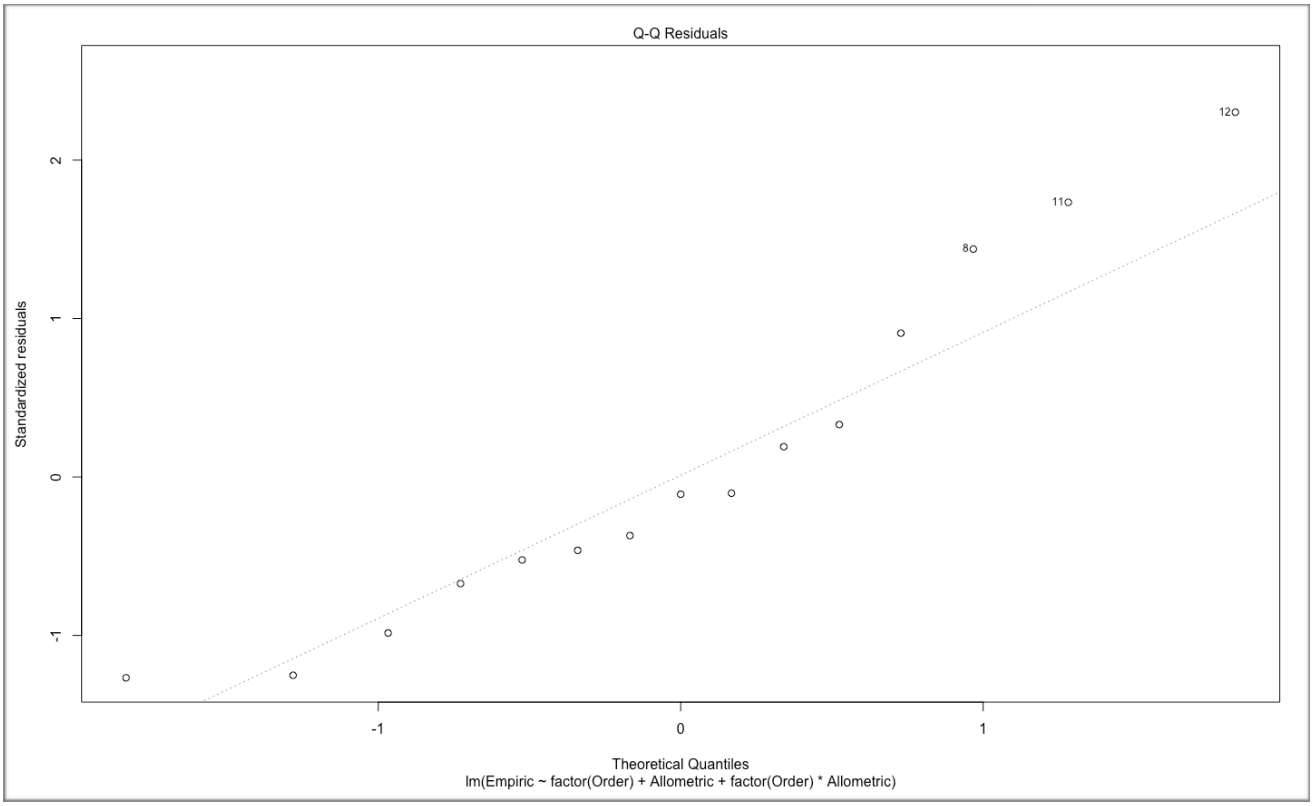



Plot to check the normality of errors.

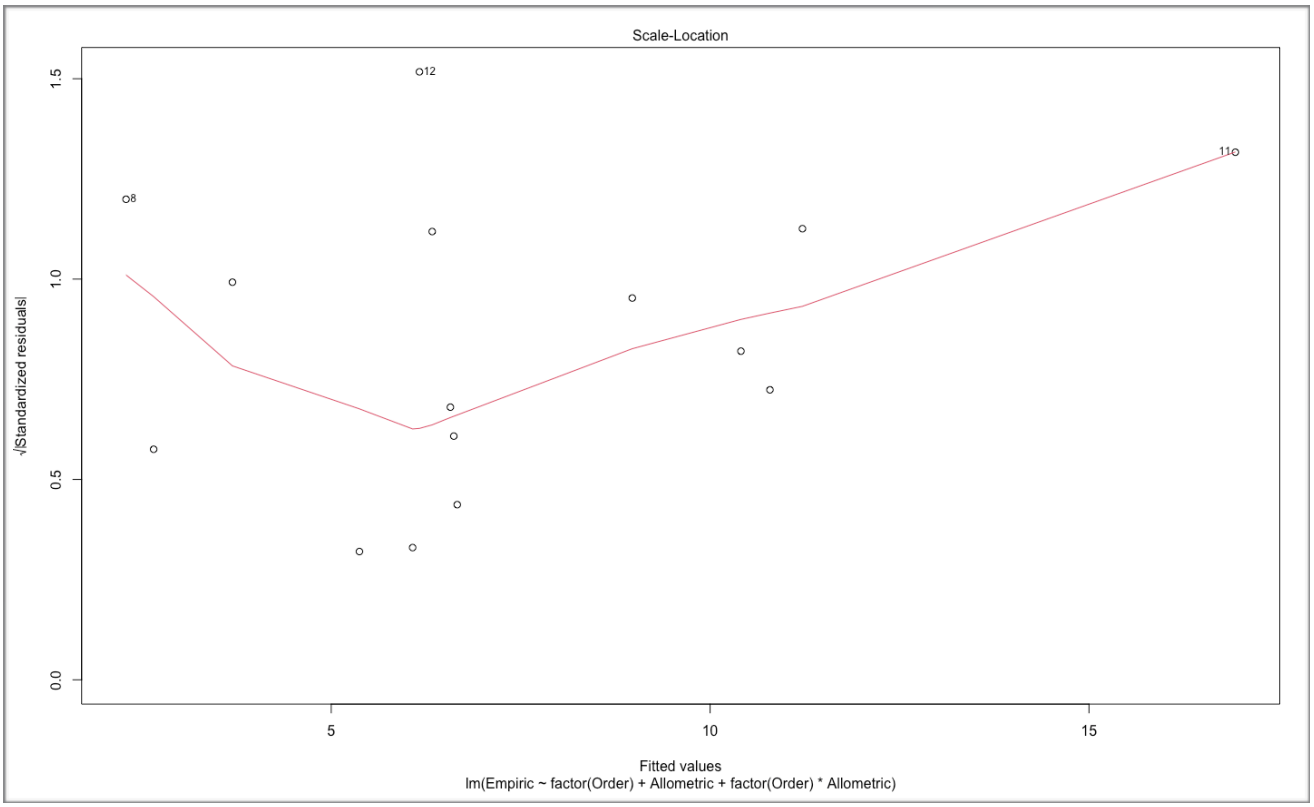
## Appendix 8 : Diagnostic plots for the prediction of empirical average DTD estimate in function of allometric average DTD estimate



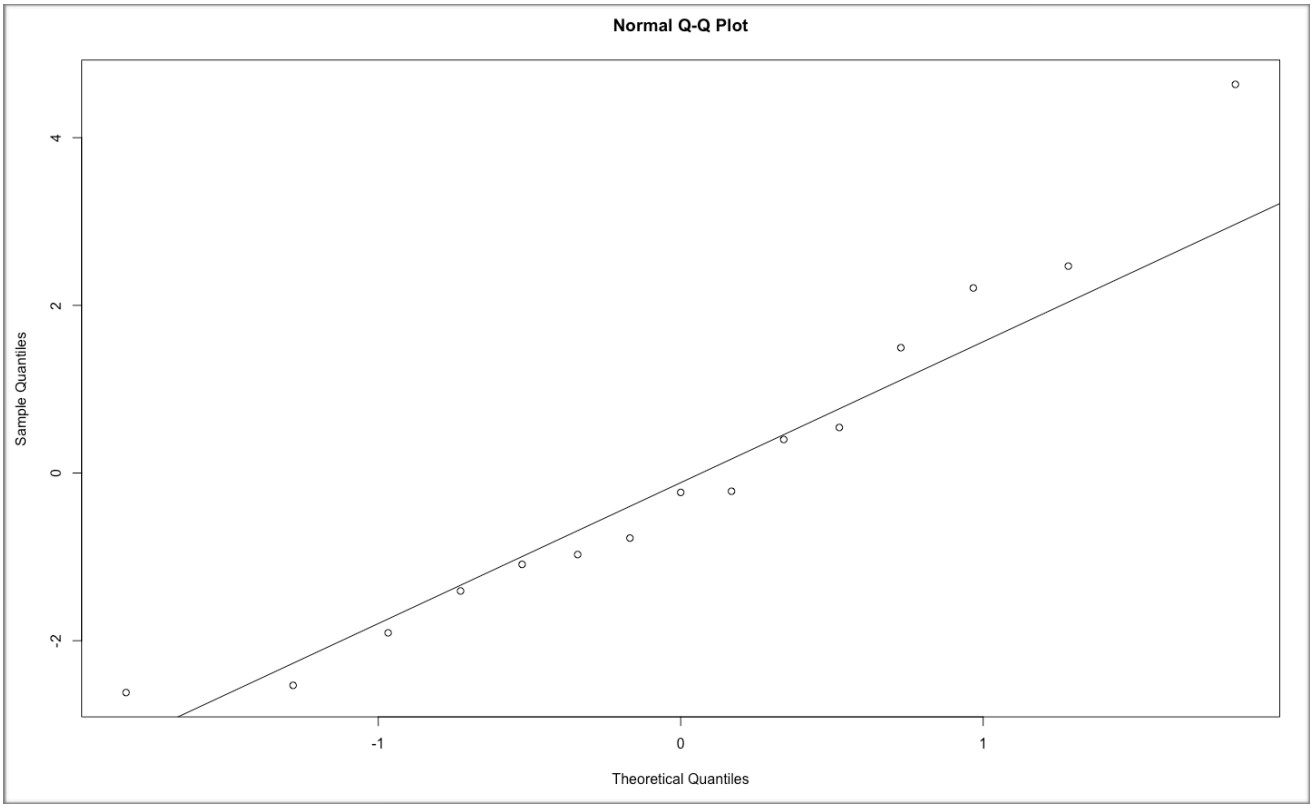

Plot to check linearity.




Plot to check the residuals.




Plot to check the homoscedasticity of errors.




Plot to check the normality of errors.