



Assessing different methods for measuring mammal diversity in two southern African arid ecosystems

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Abstract

Management and conservation actions are only as effective as our ability to monitor and assess biodiversity trends. We therefore compared the cost efficiency and effectiveness of several standard methods to assess mammal diversity using camera traps, live traps, track plates, mist nets for bats, acoustic bat surveys, spotlight surveys, and block transects recording individual animals, scat, and tracks. We also assessed local knowledge through interviews. We surveyed on two contrasting arid ecosystems in South Africa. Our data indicated that block transects were the most cost-efficient and effective method at ascertaining terrestrial mammal species richness. Depending on the goal of the study and the area, a combination of block transects with camera traps or spotlight surveys is a viable option. However, our study indicated the best combination to detect species across different taxonomic groups was block transects and live traps. Local knowledge interviews can be a good addition to a survey as it assesses mammal diversity for longer time period and not just the survey season and it provides knowledge on species that are difficult to detect.

Keywords Mammal diversity · Monitoring · Transects · Camera traps · Spotlight surveys · Indigenous knowledge

Introduction

Human impacts on the environment have caused us to enter a new era, called the Anthropocene, in which biodiversity loss is considered one of the most critical environmental issues (McGill et al. 2015; Steffen et al. 2015). The loss of biodiversity has significant implications for ecosystem health and threatens valuable ecosystem services and human well-being (Chapin et al. 2000; Ceballos et al. 2015; Drouilly and O’Riain 2019). To better understand how mammal

communities change in response to anthropogenic factors, information on their diversity and community composition is required (Malcolm and Ray 2000). Furthermore, the knowledge and monitoring of the presence, population size, and distribution of species are necessary for planning and evaluating conservation strategies (Corlatti et al. 2016; Hackett et al. 2007). Effective management is linked to well-designed monitoring systems, which require constant monitoring, to allow for adaptive management and planning (Kerley et al. 2003; Di Minin and Tuuli 2015). Diversity surveys are time-consuming, expensive, invasive, and usually limited to surveying certain taxa (Burton et al. 2015). Biodiversity surveys, especially on a large scale, are difficult to perform due to these limiting factors and the cost and resources needed for keeping them up to date are high (Leempoel et al. 2019; Di Minin and Tuuli 2015). The current biodiversity crisis is calling for developing reliable and rapid, straightforward, and multispecies methods to determine and monitor diversity and species richness across a wide range of landscape characteristics (Kerley et al. 2003; De Bondi et al. 2010; DeWan and Zipkin 2010; Burton et al. 2015; Rockhill et al. 2016).

There is a plethora of different survey methods and choosing the correct one is key to providing the relevant data for research and conservation interventions. Most methods target

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certain types or sized animals, but even then some species are not detected (Hackett et al. 2007). However, many studies have concluded that survey methods can be complementary and it is advantageous to combine different methods (Gompper et al. 2006; Leempoel et al. 2019; Rockhill et al. 2016; Torrents-ticó et al. 2017). Criteria to select the most appropriate method or combination of methods need to be defined, accounting for the characteristics of the study area and taxonomic group under investigation (Swan et al. 2014). One of the main factors restricting research and monitoring is financial cost. Not only does the effectiveness of methods need to be assessed, but also the cost and time efficiency in terms of species/individuals detected per effort unit (Gardner et al. 2008; Waudby et al. 2019). An effective method should detect not only the most species possible, but also the most taxonomic groups, and do so in a cost and time-efficient manner. The assessment needs to realistically incorporate the cost of equipment (Villette et al. 2016) and the cost per distance traveled (Gaidet-Drapier et al. 2006) while also assessing the species detected and the range of taxonomic groups detected.

Here we compared the effectiveness and efficiency of different mammal diversity assessment methods in two arid ecosystems, as well as discuss their specificities and complementarity. Here we used standard field methods such as block transects, camera traps, track plates, spotlight surveys, mist nets, acoustic surveys, and live traps for a wide range of taxa, and also included the use of local knowledge in the comparison. We assessed the cost efficiency by determining the cost per species detected for each method and the efficiency of each method to estimate species richness by using species accumulation curves to observe when the curve starts to asymptote. The effectiveness was determined by the species richness of the method compared to the number of species in distribution range, as well as the range of taxonomic groups the method detected. In the “Materials and methods” section, we discuss each method that we used and their advantages and disadvantages.

Study area

South Africa is highly ranked in biodiversity and there are approximately 300 terrestrial mammal species in southern Africa, of which approximately 33% are endemic to the sub-region and of those, 41 are restricted to South Africa (Drouilly and O’Riain 2019). Of the mammal species in southern Africa, 57 (17%) taxa are threatened (six Critically Endangered, 20 Endangered, 31 Vulnerable), 35 (10%) are Near Threatened, and 7% are considered Data Deficient (Child et al. 2017).

We surveyed in two arid ecosystems in South Africa, the southern Kalahari in the Northern Cape Province and in the Nama-Karoo in the Eastern Cape Province. In both

ecosystems, we surveyed two different land-use types, game reserve as well as livestock areas.

Kalahari

We surveyed in the semi-arid savanna of the southern Kalahari, on the Khomani San Community Land in March 2019. The southwestern section of the Kalahari is the driest part of the region with an average rainfall of 150–300 mm per annum (Kepe et al. 2005; Wasiolka and Blaum 2011). The highest rainfall occurs from January to April, with a peak in March (Spies 2016). Temperatures range from winter lows of -10°C to summer highs of up to 45°C (Spies 2016). The predominant land use outside the Kgalagadi Transfrontier National Park is characterized by mixed grazing of sheep (*Ovis aries*), cattle (*Bos taurus*), and goat (*Capra hircus*) (Wasiolka and Blaum 2011). Topographically the area can be divided into dunes (dune crests and dune valleys), sandy plains on red to pinkish sand, and the rivers and pans (including terraces and calcrete outcrops) on whitish, compact calcareous sand and clay (Wasiolka and Blaum 2011). Auob Duneveld and Gordonias Duneveld dominate the vegetation in the Kalahari study area, with patches of southern Kalahari Salt Pans, Gordonias Kameeldoring Bushveld, Nossob Bushveld, and southern Kalahari Mekgacha (Mucina and Rutherford 2006). We surveyed along corresponding vegetation types on two land uses in the Khomani San Community Land on the livestock farmland Miershoop Pan (26.828292 S, 20.598056 E) and Erin Game Farm (26.954776 S, 20.675567 E).

Nama-Karoo

The survey in the Nama-Karoo in the Eastern Cape Province took place in October 2019. The vegetation types are the Camdeboo Escarpment Thicket, Southern Karoo Riviere, and Karoo Escarpment Grassland (Mucina and Rutherford 2006). The dominating vegetation type is low to middle-height shrubland with drought-resistant grasses becoming more abundant on sandy and silty bottomlands (Spies 2016). The geology and soil are flat or gently sloping pediments composed of mudstone and resistant sandstones (Mucina et al. 2006). The topography of the study area extends from the open Karoo plains to the escarpment forming Sneeuwberg mountain range and is transected by the Melk and Apieskloof river valleys (Martin 2017; van Cauter et al. 2005). The rainfall is mostly in the late summer and early autumn, with the main peak in March, and the winters are relatively dry (Mucina et al. 2006; Pond et al. 2002). The overall mean average precipitation is 250 mm (Mucina et al. 2006). The temperature ranges from 38°C during the peak high in January and -0.3°C minimum during the peak low during July (Mucina et al. 2006). We surveyed on similar vegetation

types on two land uses in the Karoo, Samara Game Reserve (32.440188 S, 24.734837 E) and De Nuk Livestock Farm (32.331872 S, 24.674334 E).

Materials and methods

Each survey was completed in 12 days using seven different standard methods. The methods included live traps, track plates, camera traps, spotlight surveys, block transects recording individual animals, dung, and tracks, mist nets, and acoustic surveys. Prior to the 12-day survey, we conducted interviews to assess local knowledge. The number of days we surveyed was determined by the recommendation that track plates should be set for a minimum of 12 days (Zielinski 1995). All research was done with the relevant ethical approval, H19-SCI-NRM-001, A18-SCI-SNRM-001, and permits, CRO 154/19CR, CRO 155/19CR, and FAUNA0648/2018.

Live traps

Live traps have been used to successfully estimate small and medium-sized mammal species richness, composition, and abundance across ecological gradients (De Bondi et al. 2010). Live traps are considered the key technique for monitoring small mammals (Scott et al. 2005; Torre et al. 2010). Trapping provides an accurate identification of the species and the opportunity to take samples and gather other demographic information (Harrison et al. 2002; De Bondi et al. 2010). However, most trapping methods are biased and target certain species as capture success depends on many factors such as type and size of trap, type of bait used, and the microhabitat selected and climate (Hoffmann et al. 2010; Kiwia 2006; Lambert et al. 2005; Yarnell et al. 2007). Using live traps is labor-intensive, time-consuming, and may be restricted by costs and logistics, the potential to capture the target species, or by the risk to the animal (Scott et al. 2005; Gompper et al. 2006; De Bondi et al. 2010; Villette et al. 2016). The information that comes from live trapping is such that it outweighs the costs associated and, when feasible, live trapping should be included in surveys when possible, as recommended by Rockhill et al. (2016).

We used $7.6 \times 8.9 \times 22.9$ cm Sherman folding aluminum traps (H.B. Sherman Inc., Tallahassee, FL, USA) and standard humane cage traps (SHC traps) (Global Supplies, Illovo, South Africa) $75 \times 30 \times 30$ cm to capture small and medium-sized mammals. We set five 100-m transects in each land use, giving us a total of ten transects per location. Ten Sherman traps were placed approximately 10 m apart and two SHC traps were placed along the same transect, one at the beginning and one at the end of each transect ($n = 100$ Sherman traps total, $n = 20$ SHC total). Traps were checked in the morning, then closed for the duration of the day, and

reopened in the early evening in order to avoid heat stress. When trapping in the Kalahari, we moved our transects half-way through the survey to avoid repeated disturbance from carnivorous animals that habituated to raiding the Sherman traps (Watson and Watson 1985). In the Karoo, the trapping transects were kept in the same place the full 12 days.

Track plate and sand plot

Track plates are a relatively new method, especially to southern Africa. The method was originally developed to monitor rodent abundance in the USA and then further adapted to survey for elusive carnivores (Zielinski 1995). Track plates have been used successfully in other countries, from semiarid areas of India to seasonal floodplains of Pantanal (Olifiers et al. 2011; Vanak and Gompper 2007). There are two main types of track plates, enclosed track plates or unenclosed track plates (commonly referred to as sand plots), and within those types, there are lots of adaptations, including exploring using different mediums (Olifiers et al. 2011; Zielinski 1995). Track plates can be an effective and cost-efficient method that has detected elusive and hard to survey species in other studies (Drennan et al. 1998; Connors et al. 2005; Hackett et al. 2007; Hoffmann et al. 2010). However, some species are wary of the artificial medium track plates (Gompper et al. 2006; Vanak and Gompper 2007). The use of track plates can be limited as it can be difficult to distinguish between some species tracks or difficult to identify tracks, such as small mammals, and there could be environmental damage to the plates, or constant detection of non-target tracks (McCleery et al. 2014).

We set out two types of track plates, an open sand plot and an enclosed chalk box. The sand plot was a designated plot in the sand checked and swept daily with a broom. The enclosed chalk box had a wooden track plate which comprises chalk at the open end and then sticky paper (Con-tact paper) in the middle before the bait at the enclosed end of the box, so the animal first walked on the chalk and then over the sticky paper, transferring a print of its track on the paper before getting to the bait. We modified the carbon-sooted aluminum track plate (see Zielinski 1995), using chalk instead (also see Drennan et al. 1998). In the Karoo, we diverged more from Zielinski (1995) and made a tunnel with two open ends, rather than a one end closed box, by placing two track plates back to back. Two track plates of each type were placed on the live trapping transect at the 30 m and 70 m mark ($n = 20$ sand plot, $n = 20$ chalked track plate). We checked the track plates daily and recorded and identified any tracks present.

Camera traps

The use of camera traps has become an increasingly popular method as the technology has improved and the costs have decreased, allowing the insight into animal distributions,

activity patterns, and behaviors (McCleery et al. 2014; Tobler et al. 2008; Villette et al. 2016). Camera traps can collect data on a wide range of species, which is important with the current demand for multispecies monitoring (Burton et al. 2015). There are different types of camera traps and different settings within the models, and selecting the right camera model and settings for the research objective or monitoring is important (Meek et al. 2015). Other factors, such as vegetation structure and composition, the ability to identify similar-looking species, the body size of the animal and the behavior, or wariness, of some animals also influence the success of camera traps (Bowler et al. 2017; Meek et al. 2015; Torrents-ticó et al. 2017; Valente et al. 2018).

Camera traps can run continuously for long periods, perform in most vegetation types and structures, withstand most weather conditions, and cover a wider area than other methods (Bowler et al. 2017; De Bondi et al. 2010). Camera traps have a large initial investment cost, but can still be a cost-effective method (Gompper et al. 2006; Rockhill et al. 2016; Villette et al. 2016). Camera traps are time efficient in field as the maintenance hours of camera traps are low, but high personnel hours are needed for data processing (McCleery et al. 2014; Torrents-ticó et al. 2017). However, there is current research into lessening the data processing time, like using citizen science and artificial intelligence (Green et al. 2020; Swanson et al. 2016; Pardo et al. 2021). Camera traps are commonly used to monitor medium to large-sized mammals and have been found to be effective at detecting nocturnal, threatened, or cryptic species (Bowler et al. 2017; De Bondi et al. 2010). Camera traps are rarely used for small mammals, which is likely due to the difficulty in identifying similar small mammal species, but have been modified to detect small mammals in some habitats (De Bondi et al. 2010; McCleery et al. 2014). However, it may not be possible to detect species of all body sizes as setting camera traps to target small mammals influence the capacity to detect larger mammals, and vice versa (Swan et al. 2014).

Our assessment overlapped with camera traps deployed for the Snapshot Safari project (Pardo et al. 2021), using Cuddeback (Cuddeback Digital, Green Bay, WI, USA) Black Flash (model# 1231) and IR Plus White Flash (model# 1309) camera traps. The camera traps were positioned on a tree or pole within a 250-m radius of a predetermined GPS point at the center of a 5-km² grid cell. Cameras are placed ~50 cm above ground facing the nearest game trail. In the Kalahari, we used 18 camera traps ($n = 10$ on Erin, $n = 8$ on livestock area) and in the Karoo, we used 17 ($n = 8$ in Samara Private Game Reserve, $n = 9$ on De Nuk Livestock Farm).

Spotlight surveys and block transects

For many species, direct counts are impractical, and so researchers must rely on indirect signs such as tracks and scats

(Stephens et al. 2006). Walking transects looking for tracks and scat are beneficial because these surveys are simple to implement, time efficient, and sample the entire active period of target species (Edwards et al. 2000). While transects can be time efficient, they can also be labor-intensive depending on the terrain and distance needed to walk (Bowler et al. 2017). The success of transects looking for tracks requires soils that can take and hold a clear print, as track quality can degrade making the chance for misidentification greater (Harrison et al. 2002; Stephens et al. 2006). Some species also bury their scat which would make detectability difficult (Edwards et al. 2000). Transects have been found to be an effective method to detect medium and large mammals (Harrison et al. 2002; Gaidet-Drapier et al. 2006; Gompper et al. 2006).

Spotlight surveys are a widely used method for assessing nocturnal mammals (Scott et al. 2005). Spotlight surveys are used for different taxa like cervids, lagomorphs, carnivores, crocodiles, and fish. It is one of the most popular field methods to assess deer abundance in Europe (Corlatti et al. 2016). The success of a spotlight survey is largely dependent on if the animal looks towards the spotlight, to see the reflection of their eyes. The vegetation structure, moonlight phase, and the number of drivable roads also affect species detection while doing a spotlight survey (Edwards et al. 2000; Harrison et al. 2002; Ruelle et al. 2003; Scott et al. 2005).

We conducted spotlight surveys along roads within our study areas, with observers with spotlights scanning in opposite directions in the back of a 4 × 4 vehicle ($n = 10$ total surveys in the Kalahari, $n = 11$ in the Karoo). The survey started after sunset and ran 10 km in length in the Kalahari but only 5 km in the Karoo (due to the limited size of the livestock farm).

Once a day, 2-3 observers walked block transects accompanied by Khomani San trackers in the Kalahari ($n = 33$ transects) and trackers from the South Africa College of Tourism (SACT) Tracker Academy (<http://www.trackeracademy.co.za/>) in the Karoo ($n = 36$ transects). Survey groups walked away from the drop-off point for 1.5 km, then turned 90° to the right and walked for 500 m, and then turned and walked back to the road another 1.5 km. Groups documented tracks, scat/dung, and individual sightings of any animals observed.

Mist nets

The most common method to study bats is with nets or harp traps (Kunz and Parsons 2009). Mist nets are made of a fine mesh of synthetic fibers and are usually black (Weber et al. 1991; O'Farrell and Gannon 1999). Mist nets are typically labor-intensive, can yield low returns, and require specialized training (Fleming et al. 1972; Hoffmann et al. 2010). The location of the mist nets, net height, and the number of mist nets affect the success; e.g., the more nets, the higher chance of success (Hoffmann et al. 2010). Moonlight and wind are

reported to affect the success of using mist nets, as bats appear to avoid the nets possibly because the nets are more easily detected (Hodgkison et al. 2010). Capture success decreases as the night progresses and the success declines if the nets are set up in the same spot during consecutive nights (Hoffmann et al. 2010).

Depending on the site, we used different combinations/lengths of net set-up, using two or more monofilament 716 mist nets (Ecotone, Gdynia, Poland) of varied lengths, e.g. 3 m, 6 m, or 12 m, near water points or within obvious “flight paths” using poles, alternating between the land uses. We on occasion used nets stacked on top of one another, on 4 m tall poles to increase trapping effort. We did not deploy mist nets during evenings with strong winds. When a bat was captured, it was quickly removed, placed in a cotton bag, and shortly after capture identified using identification keys (Monadjem et al. 2010; Kearney and Seamark Africanbat.org unpublished key).

Acoustic surveys

Acoustic detectors have provided opportunities for remotely surveying bats without the need to capture them (Hoffmann et al. 2010). Bat species can be identified using search-phase call sequences with varying degrees of certainty, as bats have variable intensity of vocalization among species (Vaughan et al. 1997). Many species of bats produce echolocation calls that appear to be distinctive (O’Farrell and Gannon 1999; Vaughan et al. 1997). However, there can be overlap in call parameters of sympatric species or species with similar foraging niches (Monadjem et al. 2017). Acoustic detectors survey a larger area than mist nets and longer time frame, but may not sample all species due to different echolocation calls, especially low-intensity vocalizations (O’Farrell and Gannon 1999). Both O’Farrell and Gannon (1999) and Monadjem et al. (2017) concluded that the use of complementary capture techniques in addition to acoustic monitoring was more effective at assessing the full bat species richness in study areas.

We did acoustic bat call surveys using long-duration field recordings from Song Meter SM4 recorders (Wildlife Acoustics, Maynard, MA, USA). We set up three recorders among the two land uses on a tree, 1.5–2 m above ground level near a water source in each of the land use recording in full spectrum (*.wav). Each detector started recording 30 min before sunset and stop recording 30 min after sunrise. They were moved every 2–3 days to survey across the land use.

Local/indigenous knowledge

Human communities living in and around protected areas often have important ties with those areas, giving them a particular knowledge about that area (Gandiwa 2012). The use of local knowledge in wildlife management, conservation, and

research has been practiced for decades (Evangelista et al. 2018). Ecological knowledge can be particularly useful when managing wildlife populations in remote locations where other methods may be impractical (Gilchrist and Merkel 2005). Local knowledge can be assessed through semi-structured interviews, questionnaires, analytical workshops, and collaborative field work (Evangelista et al. 2018). Integration of indigenous knowledge can lead to a better understanding of system dynamics, as they could be able to determine changes (Jevon and Shackleton 2015). Hellier et al. (1999) concluded that rapid surveys of indigenous knowledge could be used as a source of information about trends in biodiversity, including changes in abundance of species and dynamics of different vegetation types.

Knowledge is unevenly spread through societies and local knowledge is held by individuals and not groups (Chalmers and Fabricius 2007). Anadon et al. (2009) claimed part of the effectiveness of using local ecological knowledge was picking the ideal group of informants. There were inconsistencies between randomly picked participants’ understanding and that of local experts and scientists, the randomly selected people did not have the same knowledge as the local experts (Chalmers and Fabricius 2007). The variability in local ecological knowledge could be due to different levels of environmental awareness in the study community and also the extent of human-wildlife conflicts (Gandiwa 2012).

To assess local knowledge, we interviewed 20 people in the Kalahari and 22 people in the Karoo. The interviews were guided by a set of cards of each mammal species potentially occurring in these areas as extracted from Stuarts’ Field Guide to Mammals of Southern Africa. The mammal card sets included 77 species in the Kalahari and 82 species in the Karoo. Each card included species name in English and Afrikaans, a picture, and a reference of their tracks and sign, similar to the photo book used in Evangelista et al. (2018). We used a mix of stratified and snowballing sampling approach to access experts with different experience and knowledge of wildlife in the area. In the Kalahari, we interviewed trackers ($n = 9$), rangers ($n = 1$), farmers/shepherds ($n = 2$), elders ($n = 8$), and women ($n = 6$). In the Karoo, we interviewed various staff members at Samara lodge ($n = 10$), trackers from the tracking academy ($n = 5$), and the farmer and farm workers of De Nuk Livestock Farm ($n = 7$). We conducted the interviews prior to the 12-day survey to avoid any biases that could arise from the trackers or staff members observing what species we detected during the survey.

Data analyses

We combined the data from both land uses when comparing the effectiveness and efficacy of the survey methods. Species richness, the number of species in the area, is the most widely used measure of biodiversity (Scholes and Biggs 2005;

McGill et al. 2015; Evangelista et al. 2018). When we assessed species richness in the Kalahari, for species in the order Rodentia that were less than 1 kg, we combined recorded presences into a general “rodent species” group as we struggled to identify the tracks, from the track plates and during the block transects, to species level. Species accumulation curves, which plot the cumulative number of species detected against the sampling effort, are frequently used as an estimate of completeness of an inventory, as the curve reaches an asymptote when all species have been recorded (Tobler et al. 2008). We used the package “nlstools” version 1.0-2 (Baty et al. 2015) in R version 2.5-2 (R Core Team 2016) to fit species accumulation curves using Michaelis-Menten and asymptotic models to observe the sampling effort of each method. We compared asymptotic and Michaelis-Menten fitted curves which both have slightly different properties in fitting the points. The asymptotic values, “ A_{sym} ” from the asymptotic model and “ V_{max} ” from Michaelis-Menten model, indicate the value in which the curve levels out, the maximum number detected with that method. The value k from the Michaelis-Menten model illustrates how long it takes to reach half the asymptotic value. For the interview data, we used number of respondents rather than days to plot species accumulation curves. We made two species accumulation curves, one from the raw interview data and another curve using filtered data in which we only kept the species that 50% or more of respondents reported were present (referred to as filtered interview data from now) to account for some bias in the answers. We calculated the proportion of species and orders by using the number of species or orders detected compared to the species present in the study area according to the distribution maps found in Stuarts’ Field Guide to Southern African Mammals.

When calculating the cost efficiency, we included the cost of fuel, equipment, maintenance, and cost of labor for each method to calculate the cost per species detected. The cost of labor was estimated with the hourly wage of \$14, based of entry level positions in the USA, and did not include post-field processing time. Cost unit was set in US dollars.

Results

Kalahari

We detected 32 mammal species with the combination of standard field methods, 28 species on the livestock area, and 28 species on Erin Game-hunting Farm; however, two species on Erin are introduced non-native species, camel (*Camelus dromedarius*) and impala (*Aepyceros melampus*). Respondents from the local knowledge interviews stated that 70 species were present and when we filtered the interviews to only include species that >50% of respondents said were present, respondents stated 34 species present (Table 1).

Block transects detected the most species of the standard field methods (Table 1). Spotlight surveys recorded the species that block transects did not detect, which was impala. Block transects were the only method to detect South African hedgehog (*Atelerix frontalis*), meerkat (*Suricata suricatta*), ground squirrel (*Xerus inauris*), and honey badger (*Mellivora capensis*). With the block transect, we recorded 30 species using tracks (Table 1), of which 11 species were not detected by dung or individual encounters. We identified the presence of 17 species using dung as evidence of presence and detected 18 species by sightings of individuals. Mountain

Table 1 Comparison of species detected and cost efficiency of each survey method in the Kalahari and the Karoo research sites and the average cost between the two sites

Survey method	Species detected in the Kalahari	Cost per species detected in the Kalahari	Species detected in Karoo	Cost per species in Karoo	Average cost between sites
Local knowledge	70	\$16.90	72	\$8.65	\$12.78
Local knowledge filtered	34	\$34.80	47	\$13.26	\$24.03
Track plate—sand plot	16	\$35.97	8	\$76.95	\$56.46
Spotlight survey	21	\$105.82	20	\$158.74	\$132.28
Block transects	31	\$156.61	29	\$199.81	\$161.71
Block transects—tracks	30	-	27	-	-
Block transects—dung	17	-	24	-	-
Block transects—individual sightings	18	-	18	-	-
Acoustic survey	8-10	\$430.57	14	\$247.40	\$338.99
Camera traps	15	\$466.67	22	\$490.14	\$457.98
Track plate enclosed	3	\$470.08	4	\$580.87	\$525.48
Mist nets	2	\$432.93	1	\$878.36	\$655.65
Live traps	7	\$1705.98	14	\$931.36	\$1318.24

zebra (*Equus zebra*) were detected by both dung and sightings, but not detected by tracks. We surveyed in the range of 13 taxonomic groups in the Kalahari (Table 2 in the [Supplementary information](#)). Block transects had the highest proportion of species and orders detected as well as a low cost of the standard methods (Fig. 1). Interviews have the highest proportion of species and orders detected and the lowest cost of all methods (Fig. 1). The combination of block transects and spotlight surveys detected 61.54% of the taxonomic groups, detected 41.89% of the species in distribution range (according to Stuarts’ Field Guide to Mammals of Southern Africa), and was \$221.16 per species detected. The combination of block transects and camera traps also detected 61.54% of the taxonomic groups, detected 40.54% of species in the distribution range, and was \$382.42 per species detected.

The values from the asymptotic models imply that we surveyed for long enough with most methods as they are similar to the values we detected; however, some methods, such as the sand plot, had higher A_{sym} values than what we detected

and therefore may have needed a longer survey length (Table 2). The k value from the Michaelis-Menten model illustrates block transects, spotlight surveys, and local knowledge interviews detected half the asymptotic value by day 1, while the other methods took longer (Table 3). The species accumulation curves illustrate the difference in A_{sym} values and how quickly the curves reached the asymptote for the standard methods (Figure 2 and Figure 3 in the [Supplementary information](#)) and the interviews (Figure 4 in the [Supplementary information](#)), which one can also see with the Michaelis-Menten model species accumulation curves (Figure 5 and Figure 6 in the [Supplementary information](#)).

Nama-Karoo

We detected 45 species with the combination of standard methods in total for the Nama-Karoo site (Table 1). For the different land uses, 33 species were recorded on Samara Private Game Reserve and 26 species on De Nuk Livestock

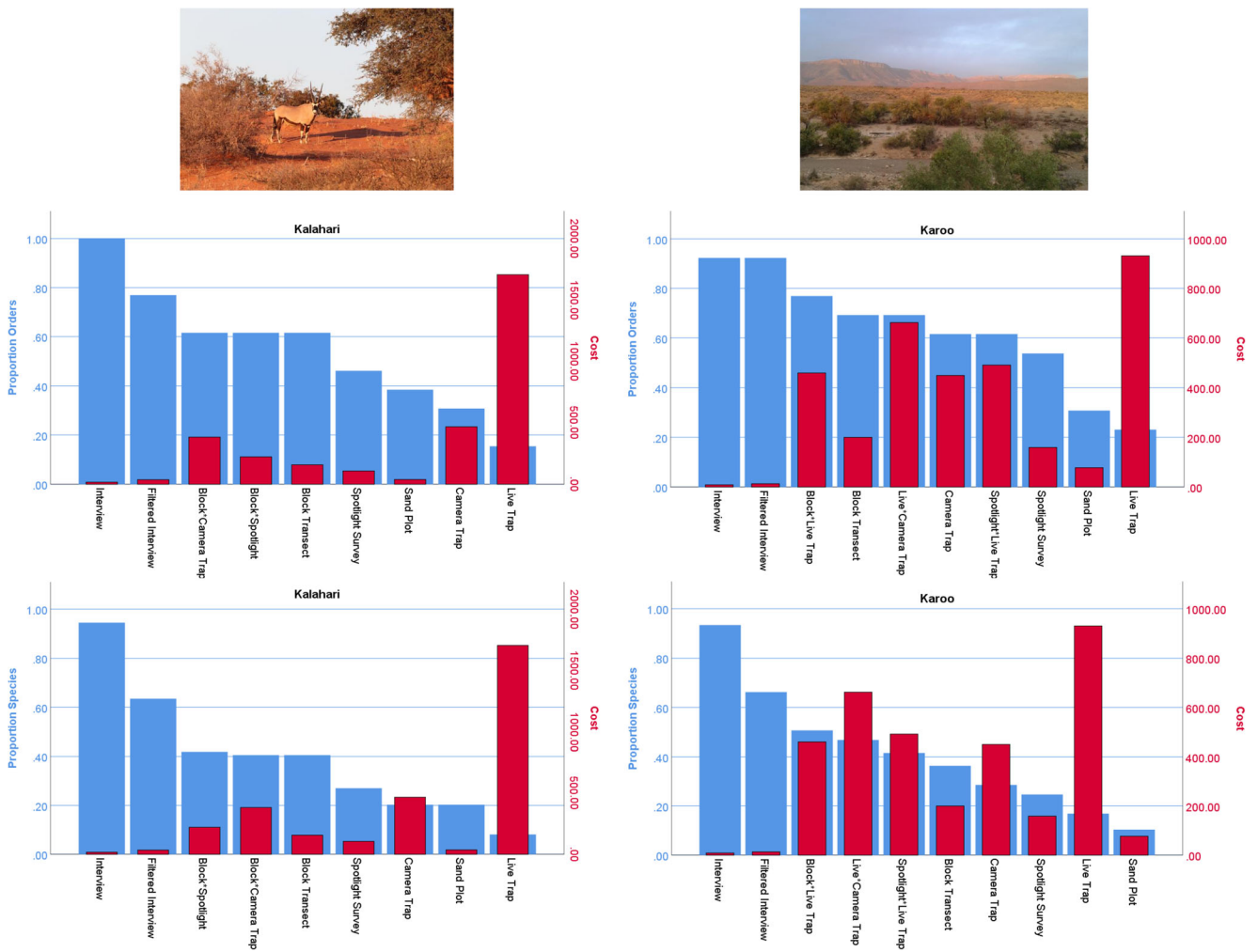


Fig. 1 Comparison of the proportion of orders detected and species to number of species in distribution range, from Stuart and Stuart (2015), in order of most effective, and the cost per species detected for all methods in the Kalahari and the Karoo

Table 2 Asymptotic model output variables for each survey method in the Kalahari and Karoo research sites including the log-likelihood value (log-likelihood), corrected Akaike information criterion (AICc), R^2 value, the asymptotic value (A_{sym}) with standard error, and the number of species detected

Survey method	log-likelihood	AICc	R^2	A_{sym}	No. of species detected
Block transects: Kalahari	-17.879	41.757	0.934	30.034 (± 0.44)	31
Block transects: Karoo	-9.285	27.571	0.937	28.842 (± 0.19)	29
Camera traps: Kalahari	-18.349	42.698	0.883	17.050 (± 1.80)	15
Camera traps: Karoo	-18.084	45.168	0.935	21.4475 (± 0.64)	22
Live traps: Kalahari	-7.887	21.773	0.912	7.441 (± 0.45)	7
Live traps: Karoo	-19.228	47.455	0.911	20.454 (± 0.07)	14
Spotlight survey: Kalahari	-13.144	32.288	0.896	20.194 (± 0.31)	21
Spotlight survey: Karoo	-18.859	46.718	0.859	21.640 (± 0.59)	20
Sand plot: Kalahari	-14.541	35.082	0.969	30.840 (± 0.09)	16
Sand plot: Karoo	-11.491	31.981	0.915	10.695 (± 2.68)	8
Local knowledge: Kalahari	-35.701	77.400	0.966	68.126 (± 0.39)	70
Local knowledge: Karoo	-55.169	116.337	0.847	69.090 (± 0.75)	72
Local knowledge filtered: Kalahari	0.4875372	5.025	0.9277	33.928 (± 0.06)	34
Local knowledge filtered: Karoo	-23.058	52.115	0.858	46.961 (± 0.11)	47
Block transect and spotlight survey: Kalahari	-16.765	39.530	0.922	30.697 (± 0.37)	32
Block transect and camera traps: Kalahari	-15.608	37.215	0.938	30.098 (± 0.34)	31
Block transect and live traps: Karoo	-22.517	54.034	0.939	39.605 (± 0.70)	41
Spotlight survey and live traps: Karoo	-23.779	56.557	0.942	34.153 (± 1.24)	33
Live traps and camera traps: Karoo	-20.104	46.209	0.973	39.844 (± 1.46)	36

Farm. Respondents from the local knowledge interviews reported that 72 species were present in the study area (Table 1). When we filtered the interviews to only include species that >50% of respondents said were present, 47 species were detected (Table 1).

Block transects detected the most species of the standard methods (Table 1). Every method, but sand plots, detected unique species that was not recorded by another method. Live traps detected 12 unique species and of those 12, eight were rodent species. Camera traps were the only method to detect caracal (*Caracal caracal*) and mountain reedbuck (*Redunca fulvorufula*). Block transects were the only method to detect black rhino (*Diceros bicornis*), black wildebeest (*Connochaetes gnou*), and southern African ground squirrel. Spotlight surveys were the only method to detect cheetah (*Acinonyx jubatus*) and red rock rabbit (*Pronolagus saundersiae*), and live traps were the only method to detect the rodent species and black-footed cat (*Felis nigripes*), cape fox (*Vulpes chama*), small gray mongoose (*Galerella pulverulenta*), and striped polecat (*Ictonyx striatus*). The combination of spotlight surveys and live traps detected 33 species and was \$491 per species detected. With the block transects, we detected 26 species by tracks, two of which were not detected by dung and individual sightings, elephant (*Loxodonta africana*) and bushpig (*Potamochoerus larvatus*). We detected 24 species when surveying for dung on the block transects (Table 1), two species that were not detected by tracks or

individual sightings, impala and yellow mongoose (*Cynictis penicillata*). We detected 18 species by sighting of individuals (Table 1) and one species was not detected by tracks or dung, blesbok (*Damaliscus pygargus phillipsi*). Species in 13 taxonomic groups can be found in the survey area (Table 5 in the [Supplementary information](#)). Block transects have the highest proportion of species and orders detected, but sand plot surveys have the lowest cost for the standard methods (Fig. 1). Interviews have the highest proportion of species and orders detected as well as the lowest cost of all the methods (Fig. 1). The combination of block transects and live traps detected 76.92% of the taxonomic groups, detected 50.64% of the species in distribution range, and was \$459.40 per species detected. The combination of live traps and camera traps detected 69.23% of the taxonomic groups, detected 46.65% of the species in distribution range, and was \$661.77 per species detected. The combination of spotlight surveys and live traps detected 61.54% of the taxonomic groups, detected 41.56% of the species in distribution range, and was \$491.38 per species detected.

The species accumulation curves illustrate the difference in A_{sym} values and how quickly the curves reached the asymptote for the standard methods (Figure 8 and Figure 9 in the [Supplementary information](#)) and the interviews (Figure 10 in the [Supplementary information](#)), which one can also see with the Michaelis-Menten model species accumulation curves (Figure 11 and Figure 12 in the [Supplementary information](#)).

Table 3 Michaelis-Menten model output variables for each survey method in the Kalahari and Karoo research sites including the log-likelihood value (log-like), corrected Akaike information criterion (AICc), R^2 value, the asymptotic value (V_{\max}) with standard error, the Michaelis-Menten constant (k) with standard error, and the number of species detected

Survey method	log-like	AICc	R^2	V_{\max}	k	Detected
Block transects: Kalahari	-9.291	24.583	0.982	33.47 (± 0.38)	0.92 (± 0.06)	31
Block transects: Karoo	-15.176	39.352	0.759	30.37 (± 0.25)	0.35 (± 0.03)	29
Camera traps: Kalahari	-17.572	41.144	0.890	19.38 (± 2.46)	5.19 (± 1.56)	15
Camera traps: Karoo	-6.964	42.929	0.943	26.30 (± 1.25)	2.33 (± 0.39)	22
Live traps: Kalahari	-10.408	26.816	0.868	9.64 (± 1.18)	3.24 (± 1.19)	7
Live traps: Karoo	-20.018	49.036	0.901	32.48 (± 14.92)	15.17 (± 10.16)	14
Spotlight surveys: Kalahari	-15.736	37.472	0.984	22.08 (± 0.671)	0.68 (± 0.15)	21
Spotlight survey: Karoo	-18.341	45.683	0.841	22.61 (± 0.92)	1.06 (± 0.24)	20
Sand plot: Kalahari	-14.920	35.840	0.968	54.77 (± 20.28)	26.98 (± 13.21)	16
Sand plot: Karoo	-12.245	33.489	0.905	17.65 (± 6.49)	13.78 (± 8.09)	8
Local knowledge: Kalahari	-40.953	87.907	0.935	73.23 (± 0.87)	0.82 (± 0.08)	
Local knowledge: Karoo	-34.407	74.813	0.974	73.93 (± 0.44)	0.797 (± 0.04)	
Local knowledge filtered: Kalahari	-8.316	22.633	0.781	34.39 (± 0.14)	0.12 (± 0.02)	
Local knowledge filtered: Karoo	-23.058	52.114	0.888	48.02 (± 0.24)	0.22 (± 0.02)	
Block transects and spotlight surveys: Kalahari	-3.360	12.719	0.990	33.54 (± 0.21)	0.68 (± 0.03)	32
Block transects and camera traps: Kalahari	-7.995	21.989	0.980	32.99 (± 0.31)	0.72 (± 0.04)	31
Block transect and live traps: Karoo	-17.197	43.394	0.971	45.06 (± 0.82)	1.21 (± 0.11)	41
Spotlight survey and live traps: Karoo	-23.231	59.462	0.922	43.31 (± 3.07)	3.07 (± 0.67)	33
Live traps and camera traps: Karoo	-21.973	49.947	0.963	47.30 (± 2.89)	3.71 (± 0.63)	36

The A_{sym} (Table 2) and V_{\max} (Table 3) values indicate we surveyed for long enough, except with live traps and sand plot surveys. The k values from the Michaelis-Menten model illustrate most methods reach the asymptote quickly (Table 3).

Discussion

The results of our study suggest that there is no single method ideal for surveying all mammal species when assessing mammal diversity. Of the standard methods, block transects, camera traps, live traps, and spotlight surveys each presented different yet efficient diversity measures. Local knowledge, although showing some variations illustrated by the 50% cut-off, was quite an efficient and effective method in our contexts.

Block transect detected the most species and was a cost-efficient method in both arid ecosystems we surveyed in. Block transects consistently detected species earlier in the surveys with over 50% of species detected by day 1. Not only did block transects detect the most species, but also detected species in the most taxonomic groups of the standard methods at both sites (61.54% in the Kalahari and 69.23% in Karoo). In the Kalahari, most species were detected by track presence, and only one species was detected by the presence of dung or individual sighting that was not detected by tracks. The success of transects using tracks is largely dependent on the

terrain, as the soils need to take and hold a clear print (Harrison et al. 2002). The Kalahari sands provided an ideal substrate to register tracks, unlike in the Karoo, and daily site checks reduced the likelihood of tracks being lost to the wind. Trained trackers accompanied the researchers which aided the identification of the tracks and dung, and the effectiveness of the survey method may have been different without the aid of a trained tracker (Anadon et al. 2009; Chalmers and Fabricius 2007).

The type of vegetation and topography played a pivotal role in the efficiency, especially of the other standard methods. Spotlight surveys detected the second most species in the Kalahari, recorded the one species which block transects did not detect, and yielded the third most species in the Karoo. Spotlight surveys also detected species quickly and were a relatively cost-efficient method, with the cost mostly being in fuel and labor costs as there is little equipment needed. If the spotlight surveys are for management purposes and not limited to a certain time or distance, then recording opportunistic observations could make spotlight surveys more effective. We noted species when driving to/from the spotlight surveys that we did not detect during the survey, such as black-footed cat. Contrary to most other studies (Vanak and Gompper 2007; Rockhill et al. 2016; Bowler et al. 2017), camera traps were not the most effective method in this current study. Camera traps detected the second most species and the second most taxonomic groups in the Karoo (Figure 12 in

the [Supplementary information](#)) but was one of the least effective methods in the Kalahari (Figure 11 in the [Supplementary information](#)) and the most costly on both sites. As the camera traps were set following Snapshot Safari South Africa's protocol, the camera traps were set to target medium and large mammals, which could be why camera traps were successful at detecting species in taxonomic groups such as Ruminantia, Perissodactyla, Primates, Suiformes, and Tubulidentata. The camera traps were less successful at detecting species in Rodentia or the smaller bodied species in Carnivora (Swan et al. 2014). Live traps were the least effective method in the Kalahari, but more effective in the Karoo. Live traps were also the costliest method; however, once the equipment is purchased, live traps are relatively low cost to service and maintain (Figure 11 and Figure 12 in the [Supplementary information](#)).

The local knowledge interviews were the most effective and incorporative and detected 12 of the 13 taxonomic groups in the Karoo and all the taxonomic groups in the Kalahari. The major benefits of local knowledge interviews are the broad range of species identified as well as the low cost of the method. In the Kalahari, respondents stated that there are 70 species present and 34 species with the filtered interviews, but we detected with the standard methods only 32 species. The filtered interviews did not detect species we otherwise reported with standard methods in the Kalahari such as slender Mongoose (*Galerella sanguinea*), bushveld gerbil (*Gerbilliscus leucogaster*), and highveld gerbil (*Gerbilliscus brantsii*), which reflects that the method has some limitations. In the Karoo, the filtered interviews did not detect 6 rodent species, which we detected with the standard methods. Studies have shown the success of local knowledge interviews largely depends on the respondents, and therefore the failed detection of the rodents could be because the knowledge of specific rodents by those we interviewed was limited (Anadon et al. 2009; Chalmers and Fabricius 2007). We also need to take into consideration that the identification of rodent species and other cryptic species can be more difficult compared to larger species. In the Kalahari, the species that the filtered interviews detected, but we did not detect with the standard methods, were either vagrant species, such as the kudu (*Tragelaphus strepsiceros*) likely from Kgalagadi Transfrontier National Park, or difficult to detect, such as the African striped weasel (*Poecilogale albinucha*), or we did not specifically survey in the appropriate habitat to detect, such as the hyrax (*Procavia capensis*). Therefore, local knowledge interviews could provide a useful source of information that includes vagrant or seasonal species that may not be present at the time of the other surveys or species that are difficult to detect.

On both study sites, the standard methods did not detect species in all taxonomic groups whose geographic distribution

range are reported to overlap with the study area (Table 2; Table 7 in the [Supplementary information](#)). To obtain the most comprehensive survey, a combination of methods and not just one method should be considered (Gompper et al. 2006; Rockhill et al. 2016). Our research in the Kalahari highlights the efficacy of block transects, but the only way to detect majority of the species is to use a combination of methods. As spotlight surveys detected the one species that block transects did not, the most effective combination was block transects and spotlight surveys in the Kalahari, which was also cost-efficient. In the Kalahari, the species accumulation curve for block transects only asymptotes on day 10 (Fig. 1 and Figure 4 in the [Supplementary information](#)); however, when combined with spotlight surveys, the species accumulation curve asymptotes on day 5 (Figure 3 and 5 in the [Supplementary information](#)). Therefore, if a rapid inventory is the object, doing block transects and spotlight surveys will yield the majority of species while still being cost-efficient. Another effective combination is the combination of block transects and camera traps; however, this combination was more costly. Camera traps can be more effective over longer periods (Leempoel et al. 2020); therefore, if the objective is long-term monitoring and if project funds allow, camera traps can be a good addition to supplement other effective survey methods, such as block transects.

In the Karoo, as live traps detected unique species in different taxonomic groups, particularly the small rodent species, the most comprehensive survey would be a combination of methods with live traps. Not only did live traps detect the small rodent species that other methods did not, but also was the only method that detected black-footed cat and cape fox. In the Karoo, the most effective combination of standard methods was block transects and live trap, which detected 41 species, was the most cost-efficient of the combination of methods, and detected the most taxonomic groups among the standard methods, 76.92% of the taxonomic groups. The three orders that the combination of methods did not detect are Afrosoricida, Eulipotyphla, and Hyracoidea. The range of Sclaters golden mole (*Chlorotalpa sclateri*) (order Afrosoricida) overlaps with our study area (Karoo) and was not detected by our methods. Furthermore, shrew species and hedgehog species (order Eulipotyphla) and hyrax species (order Hyracoidea) were not detected, as most of these species require specialized methods we did not include or we did not specifically sample in the specialized habitats. The second most effective combination was live traps and camera traps, which detected 35 species, and detected 69.23% of the taxonomic groups, missing Proboscidea as well as the other groups previously mentioned. The third most effective combination of methods was spotlight surveys with live traps, which detected 33 species, but only detected 61.54% of the taxonomic groups. The taxonomic groups this combination of

methods missed were the same as previously mentioned as well as Primates. However, it was a more cost-efficient combination of methods than live traps and camera traps.

For a comprehensive survey, we recommend to include live traps with other effective methods, such as block transects. However, if the object of the survey is to detect medium and large body-sized mammals, then we recommend a combination of block transects with camera traps or spotlight surveys. In the Kalahari, spotlight surveys were effective and cost-efficient; however, in the Karoo, spotlight surveys were not as effective. Camera traps detected more species in the Karoo and can be an effective long-term monitoring tool. Therefore, if financially possible, we would recommend a combination of block transects and camera traps for a medium and large mammal survey in an ecosystem similar to Karoo but a combination of block transects and spotlight surveys in ecosystems similar to the Kalahari.

There are a few study design considerations and potential caveats we want to highlight. On both study areas, we struggled to catch bat species with mist nets (and 3 bank harp traps in the Kalahari). In the Kalahari and the Karoo, the wind played an important limiting factor; therefore, we only mist netted for a few nights and only caught two species in the Kalahari. In the Karoo, we caught only one species and only on Samara Private Game Reserve, no species were caught on the livestock farm, yet many were seen to avoid the mist nets on evenings when we deployed nets. The echolocation data allowed the putative identification of five phonic species in the Kalahari and 7 species in the Karoo, based on species range map from Monadjem et al. (2010) and Stuart and Stuart (2015). Adams and Kwiecinski (2018) identified 12 species based on acoustic surveys in the Kgalagadi NP, some species “extra-limital” based on the printed distribution maps. The detection of only a few species could have been due to other variables, such as limited sampling or the season we surveyed or the adverse effects of El Niño influencing bat activity (Pretorius et al. 2020), rather than the lack of species present. Further research should be done to assess the effectiveness and efficiency of methods to assess bat species along with other mammal species. In the Kalahari, the detectors recorded from 18:30 to 23:00 due to battery use and to focus on the most active time of most bats. The detectors only recorded for 6 days on the livestock area and then stopped working. On Erin, it recorded for 10 days, with only two nights of data were lost. One detector in the Karoo was damaged by baboon 2 days after deployment (22 October 2019) and thereafter only two detectors were retained in Samara and the livestock area.

In the Kalahari, we detected only 3 species of rodents while live trapping, but we surveyed in the range of 29 rodents (Stuart and Stuart 2015). Other studies detected more species than what we detected (Blaum et al. 2007a; Hauptfleisch et al. 2017; Wallgren et al. 2009). Seasonality, the drought influenced by El Niño-Southern Oscillation weather system (Benkenstein 2017), or other variables such as trap type or bait

(Lambert et al. 2005; Kiwia 2006), could have influenced the low number of species detected, or it could be the areas we surveyed have a low species diversity of rodent species less than 1 kg.

The enclosed track plates were not very successful, the weather made detecting and identifying tracks difficult as wind blew sand and dirt onto the paper, covering it completely so no track prints could register. We were able to identify three species in the Kalahari and four in the Karoo, but a few we were unable to confidently identify, so it could have detected more. Track plates were one of the most expensive methods, \$580.87 per species detected in the Karoo, and \$474.08 per species detected in the Kalahari. Our findings are the opposite of previous studies that find enclosed track plates to be a cost-efficient and effective method; however, none was in southern Africa. Further studies could be done to see if different substrates are more effective and if the enclosed chalk track plates are effective in different habitats in South Africa.

The sand plots, or unenclosed track plates, were relatively successful in the Kalahari as the sand provided a good substrate to register tracks. However, positively identifying the rodent tracks was difficult, we could identify jumping mouse (which was detected by only this method), gerbil tracks, and “nag muis,” a species of mouse that we were unable to confirm the identity. Because we were unable to identify these tracks to species level, we grouped all rodent species less than 1kg into one group. Sand plots were not effective in the Karoo, even for larger mammals, as the dirt was too compact for tracks to register. One of the main benefits of sand plots is low cost, which we also found in our study on both sites. In both the Kalahari and the Karoo, both models estimated the asymptotic value to be higher compared to what we detected, and the k value was larger than 12, implying we did not survey long enough with this method to adequately assess species richness. Sand plots can be highly effective in the Kalahari or other places with good soil substrate and with a longer survey length, but further research is needed.

In conclusion, it is best to combine methods to assess mammal diversity and the combination will vary depending on the environment of the study area. Our assessment indicates that block transects were the most cost-efficient and effective method at assessing terrestrial mammal species richness, as this method detected the most species; however, it did miss species. Local knowledge interviews can be a good addition to a survey as it assesses mammal diversity for the whole year and not just the survey season and it provides knowledge on species that are difficult to detect. However, local knowledge interviews are only effective if there are people with expert knowledge. If doing a comprehensive terrestrial mammal survey with standard methods in arid ecosystems is similar to the Kalahari and the Karoo and if financially viable, the addition of live traps to block transects is recommended, as live traps

were the most effective at detecting the smaller species in taxonomic groups. Depending on the goal of the study and the area, a combination of block transects with camera traps or spotlight surveys is also a viable option.

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Author contribution Chloe Burt and Jan A. Venter conceptualized the study; Chloe Burt, Mark Keith, Chloé Guerbois, and Jan A. Venter developed and designed experiments and collected data; Chloe Burt assisted by Hervé Fritz analyzed the data; Chloe Burt assisted by Mark Keith, Hervé Fritz, Chloé Guerbois, and Jan A. Venter wrote the manuscript. All authors read and approved the final manuscript.

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Data availability Data is available on request.

Code availability Standard readily available R-codes were used and are mentioned in the text.

Declarations

Ethics approval All research was done with the relevant ethical approval, H19-SCI-NRM-001, A18-SCI-SNRM-001, and permits, CRO 154/19CR, CRO 155/19CR, and FAUNA0648/2018.

Competing interests The authors declare no competing interests.

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