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Limitations to recording larger mammalian predators in savannah using camera traps and spoor

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Traditionally, spoor (tracks, pug marks) have been used as a cost effective tool to assess the presence and in some cases the individual identity of larger mammals. Automated camera traps are now increasingly utilised to monitor wildlife, primarily as the cost has greatly declined and statistical approaches to data analysis have improved. While camera traps have become ubiquitous, we have little understanding of their effectiveness when compared to traditional approaches using spoor in the field. Here, we 1) test the success of camera traps in recording a range of carnivore species against spoor in realistic field settings (dirt roads in a South African wilderness reserve); 2) ask if simple measures of spoor size taken by amateur volunteers are likely to allow individual leopards to be tracked in the field and 3) for a trained tracker, ask if this approach may allow individual leopards to be followed with confidence in savannah habitat. We found that camera traps under-recorded mammalian top and meso-carnivores when compared with spoor in the field, with camera traps more likely to under-record the presence of smaller carnivores (civet 64%; genet 46%, Meller's mongoose 45%) than larger (jackal sp. 30%, brown hyena 22%), while leopard was more likely to be recorded by camera trap (all recorded by camera trap only). We found that amateur trackers could be beneficial in regards to recording leopard presence; however the large variance in measurements of spoor taken by volunteers suggests that this approach is unlikely to allow the collection of further information about individual leopards. Nevertheless, the use of simple spoor measurements in the field by a trained field researcher increases their ability to reliably follow a leopard trail in difficult terrain. This allows researchers to glean further data on leopard behaviour and habitat use without the need for complex spoor analysis.

The successful conservation of any species is predicated on our ability to understand its abundance and distribution (Stander 1998, Hussain 2003, Gusset and Burgener 2005, Houser et al. 2009, Trolliet et al. 2014). While some taxa (e.g. birds) have the benefit of being relatively well studied, many species such as the larger mammalian carnivores are notoriously difficult to directly monitor in the field (Stephens et al. 2006). Traditionally, indirect methods such as locating den sites, and scat or spoor (tracks, pugmarks) surveys have been utilised as a highly cost effective method (Gusset and Burgener 2005) to determine the presence or absence, abundance or population density for species such as the leopard *Panthera pardus*, snow leopard *Uncia uncia*, cougar *Felis concolor*, lion *Panthera leo*, caracal *Caracal caracal*, tiger *Panthera tigris* and pine marten *Martes martes (*Beier and Cunningham 1996, Zalewski 1999, Hussain 2003, Melville and Bothma 2006, Sharma et al. 2005, Houser et al. 2009, Sanei et al. 2011, Sheehy et al. 2014).

It has been suggested that the sex of tracked *Panthera* spp. and cougar *Felis concolor* can be judged from size differences in spoor (Bothma 1984, Stander et al. 1997, Stander 1998, Sharma et al. 2003, Sanei et al. 2011, Gu et al. 2014); indeed, if enough features are recorded, leopard, snow leopard, tiger, white rhino *Ceratotherium simum* and black rhino *Diceros bicornis* individuals may be identified from spoor alone (Stander et al. 1997, Riordan 1998, Jewell et al. 2001, Sharma et al. 2005, Alibhai et al. 2008, Balme et al. 2009). However, using spoor alone to estimate tiger densities in the field has been criticised for giving unreliable results, as simple measurements or analyses fail to provide the discrimination required (Karanth et al. 2003). Established methods were to take plaster casts or tracings of spoor on acetate from which measurements were taken (Lewison et al. 2001). Sharma et al. (2005) highlighted that data gathered in this way were of poor quality and inconsistently collected.

Most feline spoor studies have been investigated in snow (Hayward et al. 2002), tropical (Sanei et al. 2011) or clay substrates (Garcia et al. 2010), sandy loam (Lewison et al. 2001), or thick soil (Sharma et al. 2005), which are often more than 5 mm in depth. Lewison et al. (2001) found linear measurements from tracings to be more accurate in thick sandy loam. However it is not always possible to have these optimum substrate depths in more arid environments which often contain sandy substrates overlaying hard ground (but see Jewell et al. 2001). Such habitats are typical of much of the range of species such as leopard in parts of eastern and southern Africa.

Sharma et al. (2005) also found that a substrate depth of 0.5–1 cm was most effective for detecting tiger spoor and gathering data in the form of tracings and photographs, which were scanned and measured utilising computer software; a technique which has later been used for black rhino, white rhino and puma with a good level of accuracy (Jewell et al. 2001, Alibhai et al. 2008, Garcia et al. 2010). Therefore, while detailed spoor measurements can allow individual identification of some species, simple spoor measurements are considered unlikely to be reliable in determining individual identification. However, it is not clear if such measurements would allow the tracking of individuals in a single tracking period where we are more concerned with our ability to follow single individuals. If this were so, then a set of spoor that is broken due to unsuitable terrain or crossed by another individual could be reliably followed, allowing further information to be gleaned by relatively untrained fieldworkers on the movement patterns and habitat utilisation of the species of interest.

More recently, the widespread availability of camera trap technology has greatly changed the approach taken to monitoring larger terrestrial mammals of conservation concern across the world (e.g. tigers, Karanth and Nichols 1998; leopard, Trolle and Kery 2005; snow leopard, Jackson et al. 2006; Rowcliffe and Carbone 2008; ocelot *Leopardus pardalis*, Trolliet et al. 2014). Camera traps offer the benefit of allowing species identification with relative ease, and in identifying individuals for species which show variation in pelage markings or natural features (Karanth and Nichols 1998, Trolle and Kery 2005, Jackson et al. 2006, Negroes et al. 2012, Maputla et al. 2013, Pirie et al. 2014). They can have a significant advantage over indirect means of recording individuals, often allowing the population size of cryptic species (notably the large cats) to be estimated using capture–recapture models (Karanth 1995, Karanth and Nichols 1998, Trolle and Kery 2005, Jackson et al. 2006, Balme et al. 2009, Royle et al. 2009, Chapman and Balme 2010, Negroes et al. 2012, Maputla et al. 2013, Tobler and Powell 2013).

Although abundance can be estimated relatively accurately when using camera traps (Chapman and Balme 2010) providing that the probability of detection is high, cameras are positioned appropriately and camera avoidance is low (Maputla et al. 2013), there remains a lack of a standardised method of camera trap-based mark–recapture (Kelly 2008) and issues such as camera performance and efficacy have still not been satisfactorily addressed (Maputla et al. 2013, Urlus et al. 2014). However, it is detectability which presents the greatest challenge in effectively sampling the species abundance in a surveyed area (Royle and Nichols 2003) as little is known about how species vary in their likelihood of being recorded by camera traps (Balme et al. 2009, Ballard et al. 2014). In most studies the proportion of individuals which enter the camera trap range and fail to trigger the unit is unknown, resulting in under-estimation of distribution and/or abundance.

One approach is to compare camera trap results with spoor. Lyra-Jorge et al. (2008) found that compared to spoor, film cameras with a trigger delay of one second collectively under recorded by 1.65 times puma, *Puma concolor;* maned wolf, *Chrysocyon brachyurus*; mazama, *Mazama* sp; striped hog-nosed skunk, *Conepatus semistriatus*; armadillo, *Dasypus* sp. and forest rabbit, *Sylvilagus brasiliensis*. In such studies, spoor is usually recorded in sand traps, which maximises the likelihood of successfully recording a passing individual. In field work such perfect recording opportunities are rare and conditions often affect ability to record spoor (Lyra-Jorge et al. 2008, Balme et al. 2009).

In this paper we report the results of a study of large to medium mammalian predators of the African savannah, where we explore 1) the effectiveness of camera traps compared to spoor recorded in natural settings by trained amateur trackers for a variety of predators ranging in size from leopard to Meller's mongoose *Rhynchogale melleri* and 2) if observer accuracy in recording measurements and substrate depth may limit the utility of simple measurements of spoor in arid environments to track individual animals. We studied the latter using two approaches; first using a cast of a leopard print, we investigated inter-observer variation in spoor measurements. Second, using one observer following three leopards in two depths of fine sand substrate types we measured intra-observer variation in spoor measurements.

Methods

Study location

The study took place in July and August 2013 and was conducted at Thaba Tholo Wilderness Reserve, Mpumalanga, South Africa (24°57'40.4"S, 30°21'10.5"E, Fig. 1). The reserve was established in 2002 as a 1500-ha privately owned game reserve, rehabilitating land previously used for cattle with small areas used for cultivation, evidence of which still

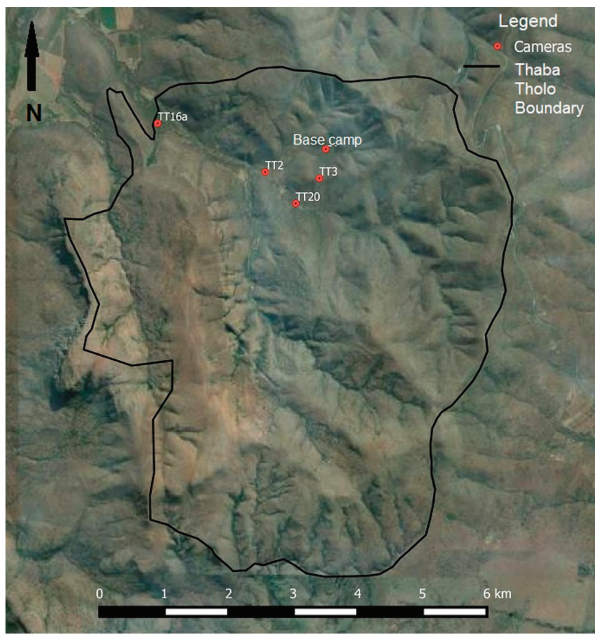

Figure 1. Map of Thaba Tholo Wilderness Reserve, South Africa showing the four camera sites which were surveyed and their relation to base camp. (Google Maps 2014 and QGIS 2.6.1).

remains. In 2009 the boundary was increased to 5400 ha and it is now run as a commercial reserve with South African giraffe *Giraffa camelopardalis giraffe*, plains, bush and mountain antelope and a number of carnivores, the largest being the brown hyena *Hyaena brunnea* and leopard.

The area is situated between the Steenkampsberg and Mauchsberg mountain ranges and lies on the cusp of two major biomes formally classified as savannah in the valleys and northern section of the reserve and grassland on top of the mountains in the southern section of the reserve. Altitudes range from 1100–2000 m and it has an average annual summer rainfall of 700–900 mm falling mainly October–February. Rock types include granite, gneiss and sandstone in the mountains with mudstone, sandstone, quartz, shale and gneiss in the valleys. The vegetation is mixed veld, predominantly *Vachellia* spp., *Combretum* spp. and *Commiphora* spp, *Themeda triandra, Hyperthelia* spp. and *Cymbopogan* spp.

Camera traps

Placement

This work was part of a wider study of the ecology of South African leopards, utilising a network of over 30 camera traps across an area of 5400 ha. Camera traps were sited along unpaved dirt roads, which tend to be used as highways by many animals (Rowcliffe and Carbone 2008).

Four sites (Fig. 1) were chosen among these to 1) maximise the likelihood of recording high numbers of predatory mammals, 2) have the correct natural substrate for spoor recording and 3) were within walking distance of base camp in order to collect data before the movement of vehicles occurred.

The cameras

Little Acorn 5210A camera traps were utilised in this study. Each camera unit had a trigger time of one second and was set to photo mode, at normal sensitivity level. The cameras have three sensors, with two requiring activation before an image is taken. The sensors detect motion and heat and can be triggered up to 15 m away. Images were taken in bursts of three and the interval between captures was set at 30 s to reduce battery depletion resulting from moving vegetation or large groups of animals passing by the site.

A single camera was placed at one side of a ‘T’ junction at four study sites, to increase the probability of capturing an animal. The camera unit was attached to a metal stake which was pushed into the ground resulting in the lens being positioned approximately 45 cm off the ground with the sensors at 40 cm. This height allowed for a range of species including meso-carnivores to trigger the sensors. The camera was angled 45° to the road to allow an animal to be in range of the lens during the one second delay between the sensors being triggered and the animal being photographed. Any vegetation which could trigger the camera or hinder the view of an animal in the image was removed prior to the survey and during monitoring. Camera sites were checked every morning, with cards and batteries being exchanged once a week. As the sites were part of a longer running study in a commercially utilised part of the reserve we felt that our activity would not impact greatly on the normal movement of animals living in the area. However to check for this we compared spoor located inside and outside of the trap zone as discussed under spoor surveys. Additionally, we compared image capture rate in weeks preceding and following the study, and found no difference in image collection rates (data not shown). Leopard, brown hyena, African civet, Meller’s mongoose, genet spp. and jackal spp. (grouped) were used in later analysis.

Spoor surveys

Spoor surveys were carried out for 38 consecutive days on foot during the early morning, by a minimum of two people who had received spoor recognition training for a week prior to the survey. This is the best time of day to locate and view tracks as the angle of the sun creates shadows in the spoor (Liebenberg 2005). In addition, recording spoor early in the morning reduced the possibility that the movement of diurnal species and reserve vehicles would damage the spoor of nocturnal animals.

Spoor of leopard, brown hyena, African civet, Meller’s mongoose, genet spp. and jackal spp. were recorded. Genet species cannot be distinguished by spoor so were grouped and there are difficulties in separating black-backed jackal *Canis mesomelas* and side-striped jackal *Canis adustus* so these were also grouped (Liebenberg 2005, Gutteridge and Liebenberg 2013). Carnivores were studied owing to the relative ease of species spoor recognition compared to that of herbivores. In addition, their generally solitary nature reduced confusion between spoor of different individuals. In order to check for camera shyness, 25 m either side of each camera trap were surveyed for spoor.

Once recording was complete, the whole survey area was swept clean of all prints by walking from one end of the area to the other, using a feather duster to sweep the whole road; ensuring spoor found the following day was fresh. The substrate was otherwise left in a natural state, open to all elements such as wind and dew, which can affect substrate conditions (Alibhai et al. 2008, Lyra-Jorge et al. 2008).

Figure 2. Representative image of carnivore spoor taken for confirmation of species identification with measurement zeroed at the back of the metatarsal or metacarpal.

Spoor which was situated within the range of the cameras took priority and was marked as being at the camera. Spoor outside this area was marked as not at the camera.

A photograph was taken with a Nikon D3100 SLR for each carnivore spoor located at all sites, with a standard mm ruler zeroed from the back point of the metatarsal or metacarpal pad in the frame for size reference (Fig. 2). The thickness of substrate was recorded as being below 2 mm or over 2 mm (rarely more than 5 mm). Only complete and clear spoor were recorded. Partial prints were not recorded to avoid misidentification. Species identification from spoor recorded in the field were checked by observers using Liebenberg (2005) and re-checked from the image by an experienced tracker. For both camera trap and spoor surveys, presence of a given species was logged once per night per location, irrespective of the number of spoor and/or images recorded.

Inter-observer variation in spoor measurements

A plaster cast of a clear leopard print was made from a spoor found in fine mudstone sand over 2 mm thick. Hairspray was used to fix the track to avoid the particles moving during the casting process. A plastic ring 35 mm high, 105 mm in diameter was placed over the track and sand built up outside in order to stop any plaster from leaking out. Baby powder was sprayed lightly over the track to stop the particles from sticking to the cast. Plaster was then poured over the back of a spoon towards the side of the ring to avoid damaging the spoor and was allowed to set for twenty minutes (A. van Loggerenberg pers. comm). The cast was used to make twenty prints in fine mudstone sand over 2 mm thick, by one individual, using similar pressure each time. Four measurements were taken (Fig. 3) directly from prints made in the substrate. All measurements were taken from the ridge made by the pad or toe indent. Each measurement was made by four independent observers using a single mm rule. Three observers were novice trackers who had been given a week's training (observers 1, 2, 4) and the fourth was the experienced field researcher (observer 3).

Measurements of spoor from an individual animal

Three separate spoor trails were found by an experienced tracker of three individual leopards walking on hard ground covered in fine mudstone or sandstone sand and each was followed for 1–2 km. If there was a break in the trail of more than five metres, the trail was considered terminated for that animal. Spoor was selected and recorded every 5 m along each trail to ensure the same individual was being measured. Hind feet were recorded due to spoor registering; where the hind foot is placed directly on the front spoor, which obliterates the spoor of the front foot (Riordan 1998, Alibhai et al. 2008). Spoor was then separated as left or right and the substrate was recorded as before and measurements taken by a single observer.

Statistical analysis

All analyses were conducted using Minitab 16 and R (<www.r-project.org>). To ensure that cameras were optimally placed and that we had no evidence of animals

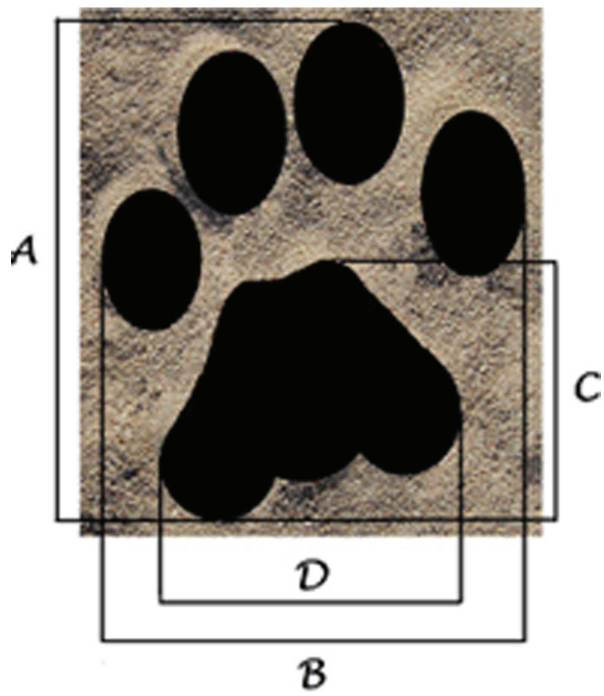

Figure 3. Spoor size was recorded in four dimensions. Full spoor length was taken as the tip of the longest toe to the furthest point of the tarsal pad (A), widest part of spoor (B), length of hind pad (C), width of hind pad (D).

avoiding camera trap locations we compared the number of spoor outside the camera trapping area with numbers located inside using a G-test. The effectiveness of the cameras in detecting each species compared to spoor was analysed using a paired t-test. In order to meet assumptions of normality, + 1 was added to the data then $\log_{10}$ transformed prior to analysis. Detection rate was calculated by dividing number of total images or spoor by number of hours of exposure (840 h; following Lyra-Jorge et al. 2008).

We investigated a possible relationship between the size and length of the study species and under-recording by camera trap compared to spoor located using the percentage difference between the two methods with a one-tailed Pearson's correlation.

A Friedman test was used to analyse the spoor measurements taken by four different observers from the same track and MANOVA was used to analyse the measurements taken by a single observer from three different animal trails in two substrate thicknesses in the field. Values for full spoor width

Table 1. Number of spoor recorded inside and outside of the camera trap area for each species during the study.

	Spoor found inside the trap area	Spoor found outside the trap area
Hyaena brunnea	15	10
Canis spp.	25	11
Rhynchogale melleri	9	8
Genetta spp.	60	23
Panthera pardus	0	5
Civettictis civetta	10	3
Total	119	60

Table 2. Number of recordings per species during the study period as camera trap images alone, spoor alone, or both images and spoor.

Species	Only images recorded	Only spoor recorded	Both spoor and image
Hyaena brunnea	4	8	3
Canis spp.	5	17	9
Rhynchogale melleri	3	8	0
Genetta spp.	8	40	11
Panthera pardus	3	0	0
Civettictis civetta	1	8	1
Total	24	81	24

were analysed following Box–Cox transformation and hind pad width following Johnson transformation to ensure data met assumptions of normality.

Results

Camera trap placement

We found significantly more spoor inside the camera trap area, supporting the hypothesis that camera traps were optimally placed ($G_5 = 13.3$, $p = 0.02$; Table 1) and that there was no camera avoidance.

Camera traps and spoor efficacy

A total of 153 recordings were collected over 35 nights from the four study locations, 48 images and 105 spoor; providing a mean of 0.114 total recordings of species camera^{-1} h^{-1}. For spoor in the trap area, a mean of 0.25 species trap area^{-1} h^{-1} was recorded, suggesting that overall spoor recorded the presence of a species more than twice as frequently as the camera traps. There was no significant difference between the number of nights species were recorded using the camera traps or using spoor located within the trapping area when leopard was included ($t_5 = 2.57$, $p = 0.23$; Table 2). However when leopard was omitted from the analysis the result became highly significant ($t_4 = 2.78$, $p < 0.01$), indicating camera traps significantly under-recorded compared to spoor. Leopard was recorded on three occasions by camera trap during the study, but not by spoor inside the trap area. These were identified as study individuals MS24, MS24 and FS7. There is a significant correlation between carnivore species recorded by both methods ($R_S = 0.81$, $n = 6$, $p < 0.05$; Fig. 4) indicating that an increase in activity is detected by both methods.

Each species' mass and length (including tail where this is visible) were taken as the mean values for the male and female of each species (from Kingdon 1997 and Skinner and Chimimba 2005). The percentage difference in recording between camera traps and spoor was found to be non-significant, but there was a borderline trend with length (one-tailed Pearson $r = -0.724$, $n = 6$, $p = 0.052$; Fig. 5), suggesting that relatively short species such as the genet or Meller's mongoose may be more likely to be under-recorded than longer species like hyena and leopard.

Inter-observer variation

Of the 20 prints made, 19 were useable and in one print, measurement D was not possible due to damage during recordings. There was a highly significant difference between observers for each measurement (Table 3). The experienced researcher had a greatly reduced variation between measurements compared to the three novices.

Intra-observer variation

Hind right measurements were omitted from the analysis due to only one animal registering in substrate < 2 mm and two animals only registering in substrate > 2 mm. With the exception of hind pad width, there was a highly significant difference in all measurements between the animals and a significant difference was found between the two substrates for all measurements (Table 4) suggesting that substrate depth affects spoor size. The full spoor length was found to be the most distinct between each animal, supporting results of Sanei et al. (2011), followed by hind spoor length, with full spoor width only showing a difference in substrate > 2 mm (Table 5).

Discussion

The ability to document the presence (and potentially abundance) of species of conservation concern is of great interest to field ecologists (Karanth and Nichols 1998, Trolle and Kery 2005, Jackson et al. 2006). Understanding the limitations of the main means of recording these species is therefore of considerable importance. In this study of mammalian carnivores inhabiting savannah habitat

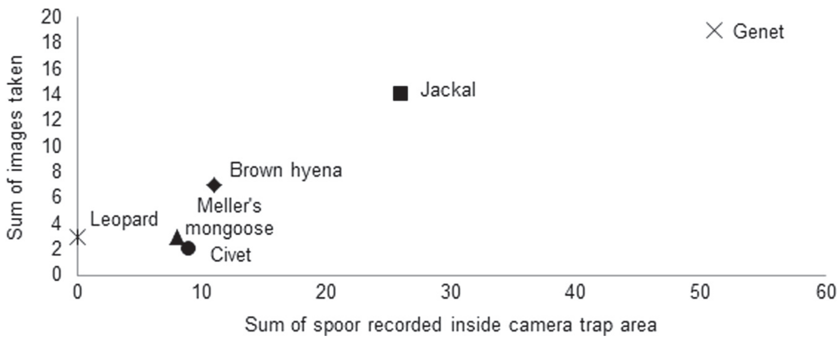

Figure 4. Sum of images of each study species recorded inside the camera trap area by spoor or camera trap images.

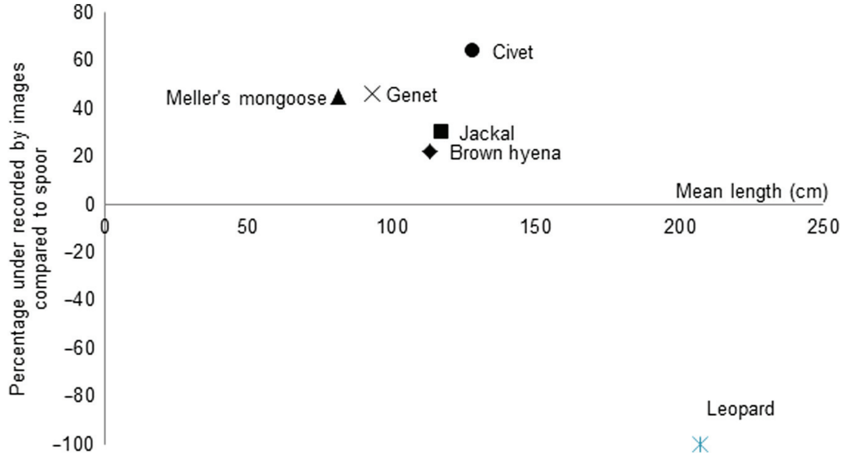

Figure 5. Relationship between study species body length (cm) and likelihood of being under-recorded by camera trap (considering the percentage difference between spoor and image records) in this study.

in South Africa, we found that camera traps significantly under-recorded the number of animals passing a trapping area when compared with those identified using spoor. This under-recording ranged from 22% for brown hyena to 64% for civet and there is a suggestion that animal size affected the likelihood of being recorded. This study illustrates that spoor can provide us with an opportunity to calibrate camera traps. However, the ability to detect and/or identify spoor is affected by the tracker's expertise as well as ground characteristics (Alibhai et al. 2008, Lyra-Jorge et al. 2008) which do need to be taken into consideration, but could be controlled where necessary.

We found that inter-observer variation in the simple measurements recorded in our study meant that spoor size data collected by amateur volunteers are unlikely to provide useful data beyond the presence/absence of leopards. However, experienced researchers were more consistent in measuring spoor, although spoor size was influenced by substrate, as well as other factors such as terrain and speed of the animal's movement (Riordan 1998, Liebenberg 2005, Sanei et al. 2011). We found that mean leopard spoor size was significantly larger in substrate with a depth of > 2 mm when compared with those recorded in < 2 mm, which may result from the greater displacement of the toes from the metatarsal pad as the foot pushes further into the substrate. Full spoor length was significantly different between animals, which was more apparent in substrates > 2 mm depth, although we advise that measurements taken directly in field are best done in < 2 mm sandy substrate as this reduces variance. This is in contrast to Lewison et al. (2001) and Sharma et al. (2005), who found thicker soil to be more beneficial for tracings and photographs, especially for digital measurements. Therefore, while simple spoor measurements collected directly in the field in sandy soil may not reliably allow the identification of individuals, simple spoor measurements of the leopard of interest can be taken, so that where the trail is broken or

Table 3. Inter-quartile and median artificial spoor dimensions (mm; Fig. 3) as recorded by four observers. Values for Friedman analyses are provided below each spoor dimension.

	Full spoor length (mm)					Full spoor width (mm)				
Observer	1 (n = 19)	2 (n = 19)	3 (n = 19)	4 (n = 19)	Total (n = 76)	1 (n = 19)	2 (n = 19)	3 (n = 19)	4 (n = 19)	Total (n = 76)
Min.	81	85	90	83	81	73	75	72	74	72
Q1.	88.5	90	92	95	90	77.5	80	75	77	75
Median	91	95	95	97	95	78	80	75	78	80
Q3.	92	100	96	100.5	97	81.5	87.5	76	82.5	82
Max.	99	105	98	106	106	86	90	80	88	90
Difference	18	20	8	23	25	13	15	8	14	18
	S = 19.92 (DF = 3) p < 0.001					S = 28.22 (DF = 3) p < 0.001				
	Hind pad length (mm)					Hind pad width (mm)				
Observers	1 (n = 19)	2 (n = 19)	3 (n = 19)	4 (n = 19)	Total (n = 76)	1 (n = 19)	2 (n = 19)	3 (n = 18)	4 (n = 19)	Total (n = 76)
Min.	39	45	45	41	39	52	50	55	53	50
Q1.	46	50	48.5	51.5	47	55.5	55	55	60	55.5
Median	48	53	50	56	51	58	63	56	63	59
Q3.	51	55	52	57.5	55	58.5	70	58.5	69	63.5
Max.	55	67	56	62	67	66	75	62	74	75
Difference	16	22	11	21	28	14	25	7	21	25
	S = 25.95 (DF = 3) p < 0.001					S = 21.28 (DF = 3) p < 0.001				

Table 4. MANOVA values for each spoor measurement (mm; Fig. 3) for three leopard hind left spoor sets taken in the field. None of the interaction terms was significant.

Variable	Effects	DF	F	p
Full spoor length (A)	animal	2, 48	37.06	0.001
	substrate	1, 48	5.36	0.025
Full spoor width (B)	animal	2, 51	5.06	0.010
	substrate	1, 51	13.50	0.001
Hind pad length (C)	animal	2, 49	17.51	0.001
	substrate	1, 49	9.37	0.004
Hind pad width(D)	animal	2, 49	1.46	0.244
	substrate	1, 49	4.68	0.036

crossed by another individual, size measurements provide evidence that the focal leopard's trail has been relocated.

Images can be recorded of the spoor for computer analysis as described by Sharma et al. (2005). The lack of optimum recording substrate could be a limitation in more arid habitats, although research conducted on white rhino spoor has been undertaken in similar environments (Alibhai et al. 2008). Nevertheless under the right circumstances, spoor may still provide additional useful information on individual leopards in terms of movement and behaviour which will prove useful in developing conservation strategies.

In contrast, camera traps readily allow identification of species and individuals when variable pelage markings are evident, and often their general size or sex can be determined. Increasing the likelihood of detecting focal species is extremely important to avoid under-recording (Maputla et al. 2013). Our work suggests that this could be a more significant factor to consider when utilising camera traps than perhaps previously thought.

Trolle and Kery (2005) found dirt roads to be more effective than game trails in capturing carnivores on camera, so we are likely to have maximised our capture rate, but evidently many individuals were not recorded by the camera traps. While the results for leopard are based on a small sample, results from our long term study (Pirie, Thomas and Fellowes unpubl.) also suggest camera traps record the presence of this species approximately twice as often as spoor. All four sites were picked partly because of the ideal substrate conditions, although these can alter between days due to changing temperatures, humidity, rainfall and wind strength (Alibhai et al. 2008, Lyra-Jorge et al. 2008). On two occasions, leopard spoor was registered outside of the camera trap zone and the leopard was photographed by the camera trap, but no complete leopard spore was detected within the camera trap zone. This is likely due to slight variations in the substrate within the camera trap zone. Partial spoor was not recorded to avoid misidentification, so was not recorded as being inside the trap zone.

Table 5. Mean and range (mm) of spoor measurements (Fig. 3) for three leopards hind left spoor, recorded under two substrate conditions in the field.

	Hind left: substrate < 2 mm				Hind left: substrate > 2 mm			
Measurements	A	B	C	D	A	B	C	D
Leopard 1								
Min.	75	61	36	44	73	55	37	45
Mean	78	62	38	46	81	63	44	48
Max.	80	62	40	50	88	67	50	52
n	4	4	3	3	8	9	8	7
Leopard 2								
Min.	85	55	45	45	89	58	45	45
Mean	87	60	47	47	93	63	52	51
Max.	90	63	49	49	97	70	58	60
n	3	3	2	2	16	15	16	16
Leopard 3								
Min.	82	60	41	43	80	61	40	42
Mean	87	62	45	46	88	69	47	50
Max.	95	67	49	51	95	76	55	60
n	13	14	14	14	5	7	7	8

Overall, under-recording appears to occur more frequently with smaller species. Previous studies (Kelly 2008, Lyra-Jorge et al. 2008, but see Negroes et al. 2012) support this view. In contrast, Urlus et al. (2014) found that larger Australian mammals were more likely to be under-recorded by camera traps. It is likely that this is as a result of the much greater size difference in their study, with smaller mammals having a more restricted home range around the traps, and their use of bait stations to attract smaller species (Urlus et al. 2014). Trigger time, the interval between sensors detecting movement and an image being taken, may also play a role in under recording given that small animals may not trigger the sensors or move more rapidly out of the capture zone once the sensors have been activated. Negroes et al. (2012) found having two cameras per station was on average 29% more effective than a single camera based on photographic rate. In addition, camera traps can vary greatly in their likelihood of capturing different species (Urlus et al. 2014, Swan et al. 2014) and understanding how equipment varies is of considerable importance.

Assessing predator abundance and distribution in savannah remains a challenge. We argue that the traditional approach of using spoor and the skills associated with tracking in the field still have a place in monitoring the larger mammalian predators of savannah habitat in two key ways. First, spoor allows us to evaluate how effective camera traps are at recording the study species; our study species were 37% more likely to be recorded by spoor than by our camera traps. This study also supports the view that camera trap studies should be calibrated against other methods (Gompper et al. 2006, Balme et al. 2009) in order to gain more accurate data to determine actual density, relative abundance and movements of species. Camera traps are beneficial but their reliability in capturing each animal that triggers the sensors is uncertain and depends on the camera model, habitat and as we show, species. Second, while it is unlikely that simple direct spoor measurements can be used to reliably identify unknown leopards due to inter-observer variation, such spoor measurements enable known individuals to be followed by experienced field trackers with some certainty, allowing researchers to link records at static camera trap locations with the wider movements of an individual. We therefore suggest that while camera traps are an exceptionally helpful addition to the ecologist's armoury, we should take care to ensure that the benefits of good field craft are not neglected.

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