

Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density

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Summary

1. Studies of large carnivore populations and, particularly, reliable estimates of population density are necessary for effective conservation management. However, these animals are difficult to study, and direct methods of assessing population size and density are often expensive and time-consuming.

2. Indirect sampling, by counting spoor, could provide repeatable and inexpensive measures of some population parameters. The relationship between true population density and indirect sampling results has seldom been described in large carnivore studies.

3. In northern Namibia the population densities of leopards, lions and wild dogs were measured through recognition of individuals and groups. Spoor counts were then conducted independently, to assess the relationship between true density and the distribution of spoor.

4. Sampling effort, both in terms of the number of roads and total road distance in a sample zone, and the intensity of sampling, had a marked effect on the accuracy and precision of spoor frequency calculations.

5. In a homogeneous habitat, leopard spoor were evenly spread along different roads and spoor frequency was independent of road length. Taking into account very low sample sizes, the spoor density of leopards, lions and wild dogs showed a strong linear correlation with true density. The slope of the regression for leopards was different to that of lions and wild dogs.

Key-words: leopard, lion, population estimate, wild dog.

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Introduction

Reliable population estimates are important in all wildlife management and conservation projects. Estimating the numbers of large terrestrial carnivores is notoriously difficult, and depends on the recognition of individuals and groups (Schaller 1972; Smuts, Whyte & Dearlove 1977) which is an expensive and time-consuming procedure. With the decline of most large carnivore populations world wide (e.g. Nowell & Jackson 1996) there is an urgent need for practical and accurate methods of estimating population numbers and monitoring trends (Caughley & Sinclair 1994).

Due to the high costs involved in direct assessments of population size, several indirect measures have been proposed. These include individual recognition of the spoor of tigers *Panthera tigris* Linnaeus 1758 (Panwar

1979), estimating population trends from spoor counts in cougars *Puma concolor* Linnaeus 1771 (Smallwood & Fitzhugh 1995) and estimating leopard *Panthera pardus* Linnaeus 1758 densities from a relationship with rainfall and suitable habitat (Martin & de Meulenaer 1988). Indirect methods of sampling large carnivore populations are often cost-effective (Smallwood & Fitzhugh 1995), repeatable and objective (Martin & de Meulenaer 1988), but are frequently criticized for being inaccurate (Norton 1990). Indirect sampling occurs mostly in areas where direct methods are not possible due to financial or practical constraints. Unfortunately, few studies have combined both direct and indirect sampling, and there is thus a general lack in understanding the results of indirect sampling, in terms of accuracy and precision.

Despite low sample sizes, this paper presents relevant data that contributes towards such an under-

standing. The true density of several large African carnivores in Namibia was determined independently by means of direct sampling. Extensive spoor counts of these species were then performed in the same area and time frame. The paper demonstrates the sampling characteristics of spoor counts, and describes the relationship between spoor frequency and true density in a semi-arid environment where carnivores live at low density.

Methods

The study was carried out in the Kaudom Game Reserve and Tsumkwe District, Namibia (Fig. 1). Kaudom Game Reserve (KGR) is 3842 km² in size with central co-ordinates of 20020'S and 20030'E. Tsumkwe District (TD), an area with no formal con-

servation status (4869 km²; 19°30'S, 20030'E) is inhabited by JujHoansi San at a density of 0.39 people km⁻². The vegetation is dominated by forest and shrub savannah woodland (Giess 1971) with *Burkea africana* (Harms), *Commiphora africana* (Rich), *Terminalia sericea* (Burch) and *Grewia* spp. as the major species. Both KGR and TD fall within the 400-500-mm summer rainfall isohyet with annual evapotranspiration equalling 2800-3000 mm, and where the climate is described as warm semi-arid steppe with temperatures fluctuating between 5 and 36°C (van der Merwe 1983). The soil, classified as arenosols, formed hard surfaced topsoil with soft interior sands, a substrate where the spotting of spoor on the road network was moderate to easy.

Between 1991 and 1995 the population sizes of lions *Panthera leo* Linnaeus 1758 and wild dogs *Lycaon*

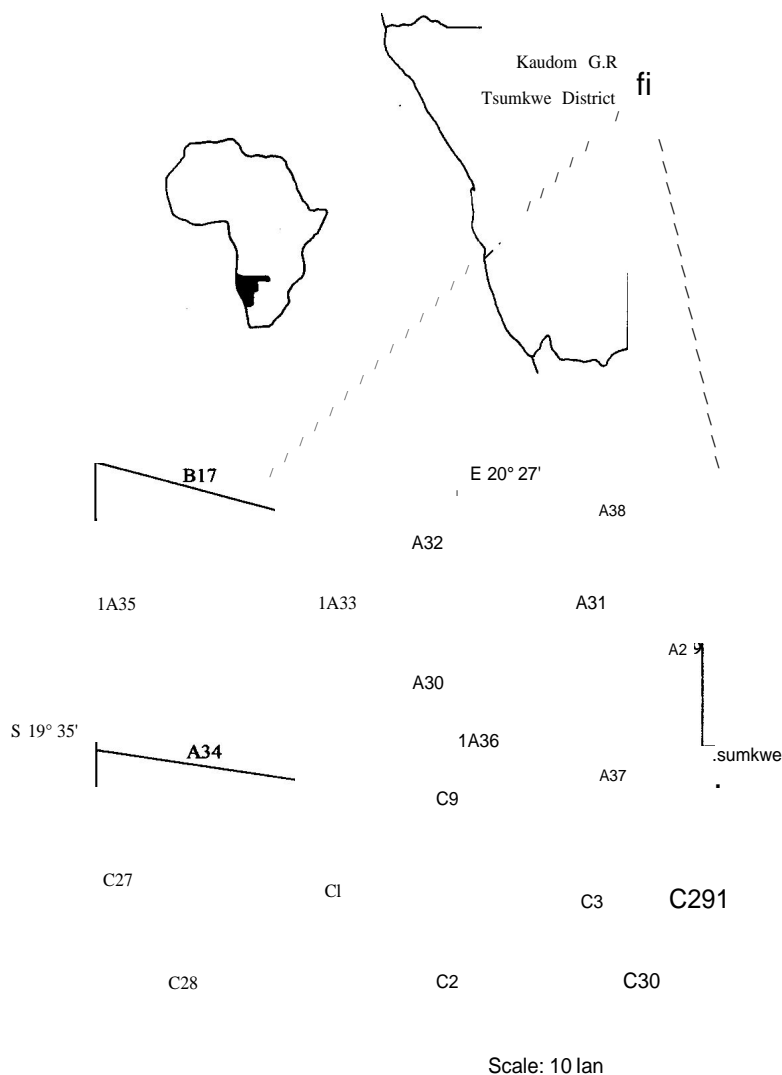


Fig. 1. The Kaudom Game Reserve and Tsumkwe District in Namibia with an outlay of a 244-km² experimental zone, and the sampling roads used for the study.

pictus Temminck 1820 in KGR and lions, wild dogs and leopards in TD were ascertained. Population size and, hence, true density was determined from the recognition and monitoring of radio-collared and marked individuals and groups. True density was estimated independent of spoor counts. All animals ($n = 86$) were immobilized following procedures described by Stander & Morkel (1991), and with a traditional San bow and arrow (Stander *et al.* 1996). Photographs were used in the recognition of 46 individual wild dogs (Maddock & Mills 1994) and 47 lions were permanently marked with an individually recognizable hot brand, while immobilized with veterinary approved anaesthetics (Orford, Perrin & Berry 1988). By the end of 1992 all the leopards in the experimental zone and, 80% of lions and wild dogs in the study areas were marked or individually recognizable. These ratios of marked and known animals versus unknown animals were maintained until the end of the study period. Eighteen leopards, 14 lions and five wild dogs were radio-collared.

Spoor counts were done throughout the study area over a period of 6 months with the help of experienced San hunters. The reliability and high accuracy of their tracking skills have been described in detail (Stander *et al.* 1997a). Relevant to the present paper are high probabilities of correctly identifying species (binomial; $P = 1.0$; $n = 147$), sex ($P = 1.0$; $n = 69$) and individually known animals ($P = 1.0$; $n = 32$) from spoor. Smallwood & Fitzhugh (1993) demonstrated statistical variation in the spoor of different individual cougars, based on shape and size discrepancies. The accuracy of the San in estimating group size from spoor of lions ($P = 1.0$; $n = 39$) and wild dogs ($P = 0.9995$; $n = 12$) was equally high (Stander *et al.* 1997a).

In the present study both direct population estimates and indirect sampling were done in three zones: KGR; a 244-km² experimental zone in TD; and the remainder of TD. The 244-km² zone, termed the 'experimental zone' in the centre of TD (Fig. 1) was selected for homogeneity in habitat and availability of roads to sample spoor frequency. The roads, in the form of 'cutlines', were made for geological prospecting, and were cut through the habitat at predetermined random locations and angles.

Roads in all three zones were scanned daily for spoor of large carnivores. An open vehicle was driven at 20 km h⁻¹ along the roads with between two and four people sitting on the bumper and sides of the vehicle scanning for spoor. The condition of the road surface, time of day and number of observers were recorded during each road sample. Only early morning observations, where the road condition was 'fresh' (surface not disturbed by other vehicle tracks, rain or wind), and at least one observer on the bumper and one on the side of the vehicle, were used for analyses. In all three zones all available roads were used to monitor spoor frequencies. Only roads in the exper-

imental zone were truly random. Some roads (10–18%) in KGR and TD followed particular vegetation anomalies. All roads were sampled at equal frequency. The number and length of roads in each zone were related to an index (penetration) of the size of the area (Table 1) to indicate the sampling effort. 'Penetration rate' is defined as the sum of the combined roads in a sample zone (KGR, TD or experimental zone) expressed as a ratio of 1 km to x km² surface area of the sampling zone. When encountered, fresh spoor was assessed for species, group size, age and sex. Observations of spoor were weighted by group size, therefore spoor refers, not to a group, but to an individual animal. 'Spoor density' is the number of individual animals' spoor per 100 km (where an individual's spoor is only counted once per day), and 'spoor frequency' is the number of kilometres per spoor.

The majority of data presented in this paper were collected in the experimental zone with a focus on leopards. All the leopards that utilized the study area were immobilized by the San using a modified traditional bow and arrow (Stander *et al.* 1996) and radio-collared. This was only possible because of the tracking skills of the San, in particular their ability to recognize individual animals from spoor. The spoor of new or unknown leopards were followed, and they were then captured and marked. The spoor of marked leopards were followed frequently and the San's ability to identify individuals was confirmed. The frequency of leopard spoor crossing a road was monitored. During 6 months the 20 roads were sampled 821 times (range 11–26 times each) providing a total sample of 3089 km. Only spoor made the previous night was recorded and the leopard's identity determined from it. An individual's spoor was counted only once per day.

The frequency of spoor on roads was assessed as a possible index of the true population density, and the sex of the animal producing the spoor was used as an index of the sex composition of the population. Sampling intensity was worked out using bootstrap analyses (Sokal & Rohlf 1995) by randomly selecting two samples and increasing the sample progressively to 4, 6, 8, ... x , with fresh means, coefficient of variance and 95% confidence intervals calculated each time (Grieg-Smith 1957). The data were then plotted against the sampling effort (e.g. Figs 2 and 3). Sampling intensity was determined arbitrarily at the point where the coefficient of variance reached an asymptote and did not improve markedly with an increase in sample size (Grieg-Smith 1957).

Data were tested for normality (Komogorov-Smor-nov two-sample test) and the relationship between two interdependent variables were fitted by ordinary least squares linear regression. Usually an independent variable such as sample size or true density was expressed in terms of a linear function of a dependent variable, coefficient of variance or spoor frequency. Non-parametric statistics were used when data were not

Table 1. Area size, sampling effort and population densities in three sample zones in Namibia. Population densities were based on direct observations of recognized individuals and groups

	Experimental zone	Kaudom G.R.	Tsumkwe District
Area size (km ²)	244	2345	2731
No. of roads	20	24	75
Total distance of roads (km)	134	360	1025
Road penetration*	1.8	6,5	2.7
Estimates of true density (animals 100 km ⁻²):			
Leopards	1.45		
Lions		1.45 + 0.25	0,3 + 0.1
Wild dogs	0.53 + 0.25	1.20 + 0.23	

*The sum of the distances of all the roads in the area (expressed as a ratio of 1 km road: x km² surface area.

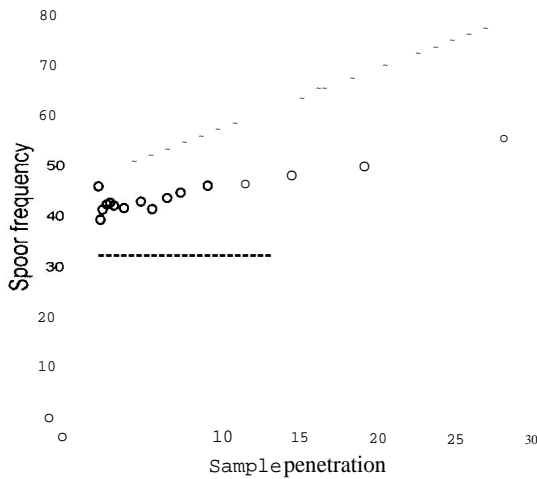


Fig. 2. The relationship between the spoor frequency of leopards (number of kilometres per individual leopard spoor) and sample penetration (the ratio of km² surface area per 1 km of sampling road) in the experimental zone. See Methods for description of bootstrapping techniques.

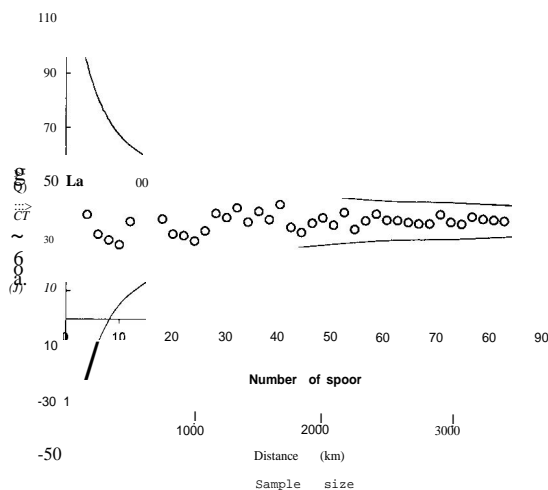


Fig. 3. The relationship between the spoor frequency of leopards and increasing sampling effort. Solid lines indicate 95% confidence intervals. See Fig.2 for spoor frequency definition.

normally distributed. Means are given with standard error ($X:t SE$) as a measure of precision. Significance was measured at $P < 0.05$; two-tailed and non-significant results are indicated by NS.

Results

LEOPARDS IN THE EXPERIMENTAL ZONE

Sampling design and intensity formed an important part of the experiments and provided an interesting approach to understanding the dynamics of spoor frequency and distribution. For leopards, the total sample of 3089 km for all 20 roads combined resulted in a spoor frequency of one leopard spoor for every 38.1 \pm 3.83 km. When separating individual roads of the experimental zone (Fig. 1) and calculating spoor frequency of each road, there were no apparent differences between roads. Average spoor frequency did not vary between individual roads ($X^2 = 15.9$; NS) nor was spoor frequency a function of road length ($b = 1.43$; $t = 1.05$; $r^2 = 0.18$; $t = 1.36$; NS.). The total length of all 20 roads gave a penetration rate of 1 km road for every 1.8 km² surface area (Table 1). Through a random selection and systematic combination of individual roads, and by calculating the ratio of km² surface area per 1 km of sampling road, the effects of an increase of sample penetration was measured (Fig. 2). After each increase in total road length and subsequent penetration rate a fresh mean and 95% confidence interval of spoor frequency was calculated. Mean spoor frequency at low road penetration did not show large variation, but error was high. When road penetration reached 1 km: 6.5 km², average spoor frequency was 41.49 \pm 8.42. This did not change much as sampling intensity increased.

Sampling analyses, for all roads combined, of leopards in the experimental zone showed that the variance of spoor frequency estimates stabilized at 30 spoor samples or 1200 km sample distance (Fig. 3). The accuracy and precision of the estimates did not

change or markedly improve as sample size was increased. At maximum sampling, leopard spoor frequency was one spoor per 38.1 km with 10.62 at 95% confidence interval. Precision, measured by the coefficient of variance (Fig. 4), increased dramatically in the first 10 samples (500 km) and an asymptote was reached at roughly 30 spoor samples. Although the coefficient of variance decreased steadily an increase in precision of only 4.6% was gained between 30 and 80 spoor samples.

The true leopard density calculation, for the experimental zone (Table 1), was based on radio tracking data of eight leopards utilizing the 244-km² zone at different intensities. The home ranges of leopards, on average 188 km² for females and 451 km² for males (Stander *et al.* 1997b), overlapped with the sampling zone to a varying extent (10-95%). The relationship between true density (based on radio tracking data), and spoor density was assessed by a separation of true density and spoor frequency data from individually known leopards. An individual leopard was selected randomly; true density was calculated based on the amount of home range overlap with the sample zone, and the frequency distribution of that individual's spoor was calculated (Fig. 5). This procedure was then repeated three times by increasing the sample size (number of individual leopards), but following a sample and remove technique to ensure independence. The four open circle data points (Fig. 5) are independent as far as individual leopards are concerned. Spoor density showed a strongly significant linear relationship with true density ($b = 1.9; t = 1.15; r^2 = 0.98; t = 12.56; P < 0.01$) when excluding the total density and spoor

frequency data point (black square; Fig. 5). This summary data point falls within the 95% confidence interval of the predicted estimate, based on the four data points, although the predicted confidence interval is much smaller than the true estimate.

The true sex ratio of leopards in the experimental zone was 1 d to 0.75 ♀ (Stander *et al.* 1997b) and the overall sex ratio of spoor observed was similar (1 d to 0.75 ♀; 95% CI = 0.062). Bootstrap analyses showed that the sex ratio estimate stabilized at 45-50 spoor samples or 1400 km sampled (Fig. 6a). Precision decreased to a standard error of 10% of the mean at 40 spoor samples and 5% at 60 samples (Fig. 6b).

WILD DOG AND LION ESTIMATES

Through direct observations, and individual recognition of single animals and groups, independent population estimates of wild dogs and lions were made in two zones, respectively (Table I). Sampling efficiency of spoor frequencies was assessed for both species in both zones, as was illustrated for leopards in the experimental zone. In all four samples coefficient of variance of spoor frequencies was equal or lower than 15% (SE as a percentage of the mean). Road penetration in both areas was high enough to account for the potential variation presented for leopards (Fig. 2). While recognizing the low samples, true density estimates of two lion and two wild dog populations appear to have strong linear interactions with respective spoor density counts (Fig. 7). The average home ranges of the two species in both populations were similar which could explain why both species

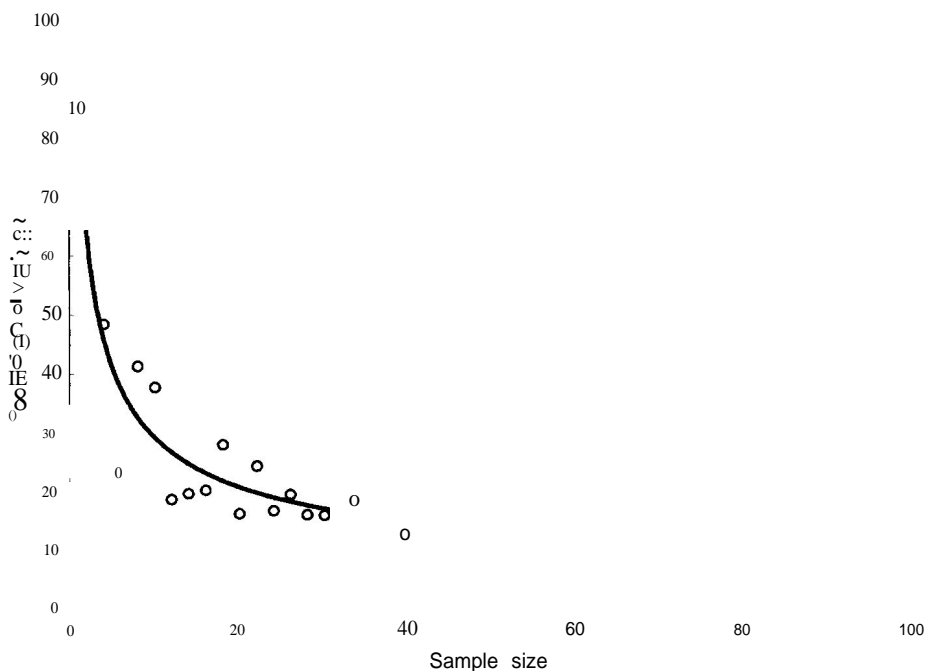


Fig. 4. The relationship between sampling precision, measured by coefficient of variance (SE as the percentage of the mean) and increased sample size.

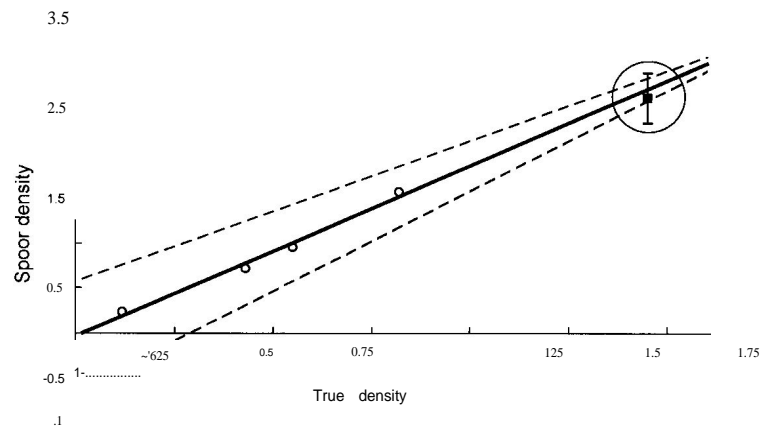


Fig. 5. The relationship between true density of leopards (leopards 100km⁻²) in four independent segments of the experimental zone population (open circles) and respective spoor density counts (spoor 100km⁻²). Dotted lines are 95% confidence intervals. The total population density and spoor density datum (black square), with 95% CI, represents the sum of the four open circle data points, but was not used in the linear regression analyses.

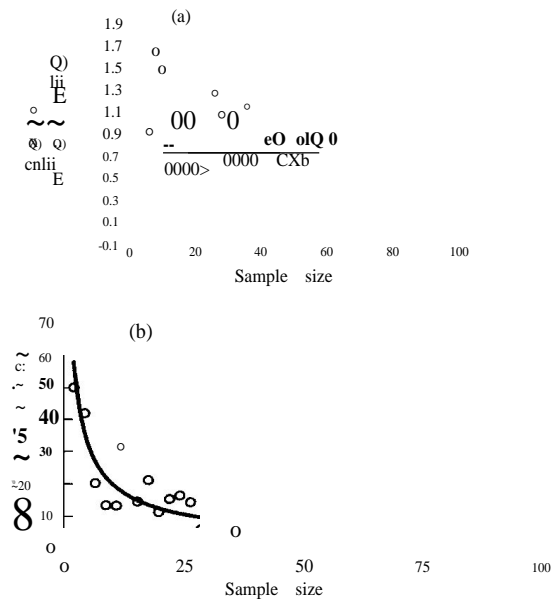


Fig. 6. The relationship between the (a) sex ratio (I male: x-female) of leopards in the experimental zone and (b) sampling precision (% coefficient of variance), with increased sample size.

showed similar relationships between true and spoor density (differences among slopes: ANCOVA; $F = 0$; $P = 1,0$). When combined, spoor density for lions and wild dogs appears to be a function of true density with strong linear properties ($b = 3.28 \pm 0.24$; $r^2 = 0.98$; $t = 13.55$; $P < 0,01$). Error margins, especially along the x-axis (true density), are large, but the relationship between spoor and true density, nevertheless, remains apparent.

The slope of the regression between spoor and true density for leopards is significantly different to that of lions and wild dogs combined (ANCOVA; $F = 12.98$; $P < 0,05$). This difference indicates that, theoretically, higher spoor density is expected for lions and wild dogs than for leopards in the event that they all occur

at similar densities. Leopards were observed to move shorter daily distances (9.7 ± 0.9 km; $n = 31$) than do lions (19.4 ± 1.4 km; $n = 16$; Mann-Whitney U-test; $U = 417$; $P < 0,001$) and wild dogs (24.6 ± 1.7 km; $n = 12$; $U = 342$; $P < 0,001$). Similarly, the home ranges of leopards were smaller than those of lions ($U = 146$; $P < 0.001$) and wild dogs ($U = 38$; $P < 0,01$). Higher spoor frequencies may be a function of range use, resulting from longer daily movements and larger home ranges among lions and wild dogs.

Discussion

Successful monitoring of carnivore density or presence from spoor counts is dependent on thorough sampling design. Determining the most efficient sampling intensity to meet the requirements is important and may vary considerably in areas of different carnivore density. Habitat utilization by carnivores is an important variable that will influence spoor counts on roads. In the uniform habitat of the present study, especially the experimental zone with random sampling roads, leopards used roads at random. Heterogeneous habitats pose more of a problem as carnivores frequent particular vegetation or geological types, and spoor frequencies on roads associated with their preferred habitats are higher than expected (Van Dyke, Brocke & Shaw 1986; Smallwood & Fitzhugh 1995).

An increase in the number of roads, or the total length of roads sampled to determine spoor frequency in a particular area has an increasing effect on the precision of the data. In the present study desired levels of precision, for leopard spoor frequency in the experimental zone, were obtained when road length (penetration) was increased to a ratio of 6,5 km² surface area for every kilometre of road sampled. Once the sampling road length has been determined, the sampling effort along those roads has further significant effects on both the accuracy and precision

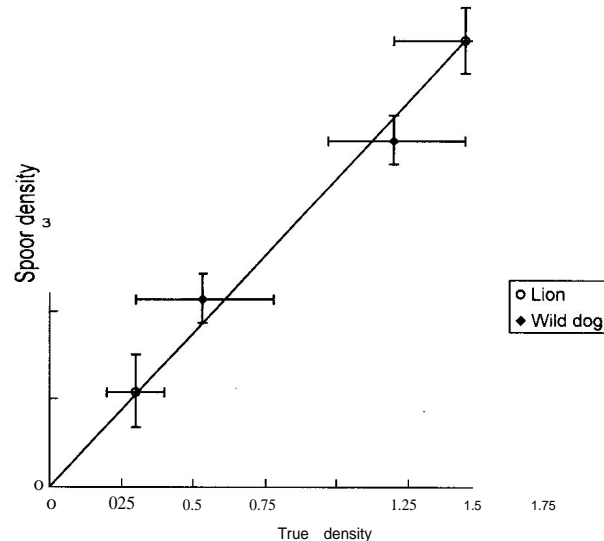


Fig. 7. The relationship between true density (animal 100 km^{-2}) and spoor density (spoor 100 km^{-1}) of two separate populations of lions and wild dogs. Both true density and spoor density are given with 95% confidence intervals.

of the spoor frequency estimates. As sampling effort increases, accuracy tends to stabilize and precision reaches an asymptote of marginal improvement with increased sample size. In the present study, such a threshold of spoor frequency estimates was reached at 30 spoor samples or 1200 km sample distance. Estimating the sex ratio of leopards from spoor required a slightly higher sampling effort to attain levels of precision similar to spoor frequency in the same zone.

An understanding of the relationship between spoor frequency and true density is of primary importance when designing an indirect measure of carnivore populations. Spoor frequency may simply be a function of range utilization or road use, but it is fair to assume that the extent of range and road use would increase under higher densities. For this reason spoor frequency under sufficient sample sizes may well be an index of true density. By double sampling, the relationship between spoor and true density may provide the means to calibrate and improve the reliability of cheaper indirect sampling techniques (Eberhardt & Simmons 1987). Double sampling, however, is expensive and time consuming, and as a result has not been performed in many previous studies.

Data from the present study show that for leopards, lions and wild dogs, spoor density is a function of true density. These relationships are strongly linear with intercepts at zero, which is encouraging since it would be fair, theoretically, to assume that zero density would result in zero spoor density. The slope of the regression for lions appears similar to wild dogs, but significantly different for leopards. This may be the result of differential range utilization illustrated by the variation in daily ranges and size home ranges. It is suggested that the slope of such regressions portray the ecological characteristics of the relationship

between spoor and true density. Assuming that the linear properties of this relationship are stable, the slope is expected to vary depending on such factors as habitat use and behaviour of species.

It is acknowledged that the sample sizes in this study are statistically extremely small, but nevertheless, it is argued that the data and analyses are of ecological and economic importance, given the high costs and effort involved. The advantages are that this approach of indirect sampling of spoor frequencies is objective, free from personal bias, is open to scrutiny and can be amended or improved as more accurate information becomes available (Mentis 1980). The use of highly skilled trackers (Stander *et al.* 1997a) in this study, especially the ability to recognize individual animals, improved our understanding of spoor distribution, but is not essential in the design of future monitoring techniques. Observers with moderate tracking skills, such as hunters, would be capable of determining the distribution of spoor along roads or transect lines. This paper, however, does not aim to provide a technique for estimating density or monitoring of trends, but to contribute towards an understanding of the relationship between spoor counts and true density.

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