

Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance

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Abstract

Population size and trends of large carnivores are difficult to determine, but are often needed to inform conservation actions. Direct counts maintained over long time periods are extremely difficult to achieve. Indices of population sizes can be used to estimate large carnivore abundances, but are often case-, species- and site-specific. Here, we test the general applicability of track-based indices to estimate large carnivore abundance. We surveyed 15 306.4 km of roads associated with 339 transects across a wide geographical scale, large range of densities and variable substrates for tracks of African large carnivores. A combined model for all carnivore species on sandy soils serves as a robust approach to predict large carnivore densities. Thus, indices based on track counts can provide useful estimates of carnivore abundance. We found consistent relationships between track densities and the actual carnivore densities, having taken account of substrate.

Introduction

Large carnivore conservation managers often face contrasting challenges in a dynamic socio-political environment. Conservationists may need to balance the need to protect populations with that of resolving human–carnivore conflict (Nowell & Jackson, 1996; Treves & Karanth, 2003; Ogutu, Bhola & Reid, 2005). For instance, African lions *Panthera leo* declined dramatically during the late 20th century (Bauer & van der Merwe, 2004), and today face many threats, most notably from farmers who persecute them for killing livestock (Ogutu *et al.*, 2005; Woodrooffe & Frank, 2005). Solutions to almost every problem, and the evaluation of their effectiveness, benefit from information on the number of individuals comprising a carnivore population. Estimating animal numbers is often practically, and technically, difficult. Several methods can be used to estimate directly the size of a large carnivore population (Mills, 1996, 1997; Gese, 2001; Packer *et al.*, 2005), but these tend to be time consuming and expensive, and often lack a measure of precision. Indirect alternatives have been used to estimate population density and demographics of large carnivores

(Smallwood & Fitzhugh, 1995; Beier & Cunningham, 1996; Wilson & Delahay, 2001; Gusset & Burgener, 2005; Balme, Hunter & Slotow, 2009; Houser, Somers & Boast, 2009). There are additional primary studies on pumas (e.g. Van Sickle & Lindzey, 1991; Smallwood & Fitzhugh, 1993; Grigione *et al.*, 1999; Lewison *et al.*, 2001) and African carnivores (Gusset & Burgener, 2005; Balme *et al.*, 2009; Houser *et al.*, 2009). There are also more reviews of this topic available (e.g. Gros, Kelly & Caro, 1996; Mills, 1997; Gese, 2001).

Furthermore, cost often constrains the frequency with which either approach can be repeated, extending the time between surveys. This is problematic insofar as it is often more important to know the changes in numbers than their absolute value.

Detecting change carries trade-offs between the precision of estimates, intervals between surveys and the risk of uncertainty during the time it takes to detect a change (Gerrodette, 1987). The few studies that have overcome these constraints relied on intensive observations over long periods (e.g. Kissui & Packer, 2004; Packer *et al.*, 2005; Durant *et al.*, 2007). More commonly, however, only a

one-off survey is available to benchmark a population at a certain date (e.g. Smuts, 1976; Martin & de Meulenaer, 1988; Stander, 1991; Creel & Creel, 1997; Gros, 2002).

The management of large carnivores could, however, benefit by using indices of the population size. Indices offer advantages in that they are generally cost effective and can be easily repeated, and can provide reliable estimates of the population size together with a measure of precision. One such approach, track counts, relies on the relationship between frequencies with which tracks (spoor) are detected and an estimate of the actual density (Van Dyke, Brooke & Shaw, 1986; Smallwood & Fitzhugh, 1995; Houser *et al.*, 2009.). Such indices may be species- or site-specific, with the type of substrate playing a key role (Standar, 1998). Thus, it is important to test their generality. For example, Standar (1998) recommended caution in extrapolating from his results to other species or areas without calibration to known populations. Some studies have combined direct and indirect sampling to define the relationship between track-based indices and actual densities (Standar, 1998; Balme *et al.*, 2009).

Here, we have developed track-based indices across a wide geographical scale in Africa, spanning several ecosystems and across a large range of densities. The diversity of ecosystems allows us to test how substrate characteristics affect track indices as a suitable surrogate for other methods of estimating population size. From this, we make some recommendations on the design of track-based surveys.

Material and methods

Study areas

We collected data on carnivore densities from seven study areas including 18 different study sites (Table 1), and combined these with published data (Standar, 1998). The different physical features of the study sites facilitated an evaluation of the effect of substrate on relationships between track-based indices and estimates of true densities. Sites in the Serengeti were surveyed in both wet and dry seasons, between which there were large differences in prey availability (Schaller, 1972; Hanby, Bygott & Packer, 1995). These seasons are considered separately.

Data collection

Track indices

The selection of transects followed the guidelines of Standar (1998), and considered substrate suitability and the extent of the area to be surveyed. Pilot studies involved driving through study sites and logging routes using handheld geographical positioning systems. Where no roads existed, such as parts of the Kgalagadi Transfrontier Park, a series of off-road parallel routes were used, separated by at least 5 km. Where existing roads were used, intersecting routes were avoided. When intersections were unavoidable, the intersecting routes were used with a minimum temporal

separation of 3 days. The logged routes in combination with digital road maps allowed us to calculate road and route lengths. By plotting routes in this way, we mapped their physical features and were able to exclude those with > 50% vegetation cover, which would have made spoor detection less reliable. We thus identified suitable sections where fine substrates such as clay and sand would allow an accurate interpretation of animal tracks.

We repeatedly drove selected sections along roads or routes – termed transects (see Table 1 for summary). When transects were driven on consecutive days, these were swept clean of tracks by towing a brush drag behind the observation vehicle. Where possible, we avoided sampling the same transect on consecutive days to minimize double counting the same track incidence. Transects were driven in the early morning and only tracks from the previous 24 h were used for analysis. Four-wheel-drive vehicles driven at an average of 10–20 km h⁻¹ served as an observation platform. A tracker, seated on the bonnet, scanned for tracks directly ahead of the vehicle. Where tracks were found, the vehicle stopped and trackers identified the species, discounting any that could not be reliably identified. Where available, expert indigenous local trackers were used and all survey teams included a competent track interpreter. We used different trackers between study areas, but each study site was directed and managed by the lead researcher concerned for the duration of the survey work. We were thus confident that our spoor indices were not confounded by observer bias (see Standar *et al.*, 1997).

Carnivore observations

Direct long-term monitoring of individuals or home-range data with known individuals formed the basis of population estimates in each study area (see Table 2). In some instances, individuals were radio-collared (White & Shenk, 2001), identified from spot or coat patterns, through photographic vibrissae dot pattern records (Pennycuik & Rudnai, 1970), or marked with unique brands (Smuts, 1976; Standar, 1991). The data collected by radio-tracking included geographic locations during weekly telemetry flights or ground-tracking.

Statistical analysis

Track indices

We defined track density as the number of individual tracks encountered per 100 km driven, where each specific set of tracks was only counted once per day. The track frequency was the number of kilometres per set of tracks. If trackers found two similar spoor within 500 m of one another and could not identify these individually, the second was not counted. We calculated both indices – track density and frequency – for each transect from which we could estimate mean values and standard errors.

Table 1 Summary of the study areas, habitat types, substrate types and effort included in the present study

Study area	Study area size (km ²)	Habitat type	Substrate type	Study site	Study site area size (km ²)	Number of transects	Mean transect length (km)	Total distance of roads	Total distance sampled	Distance per area	Mean number of times transects repeated
Tsumkwe District, Namibia ^a	4869	Closed woodland or dense shrubs	Deep Kalahari sandy soils	Tsumkwe	2731	75	3.76 ± 0.9	1025	3089	2.7	18.5 (n=821)
				Experimental	244	20		134		1.8	
Kaudum Game Reserve, Namibia ^a	3842			Kaudum	2345	24		360		6.5	
Kgalagadi Transfrontier Park, South Africa/ Botswana	15 633	Vegetated dunes and shrubby grassland		Dune-north	10 043	35	34.1 ± 1.8	1190	2146.4	8.4	1.8 (n=62)
				Dune-south	5590	21	32.5 ± 2.5	672	1334.1	8.3	2.0 (n=41)
Mabuasehube Sesatswe Mosimane Other-tree	20 135	Sparse to open tree-savanna with large areas of grassy plains		Mabuasehube	2042	16	28.2 ± 1.3	451	2002.6	4.5	4.4 (n=71)
				Sesatswe	2142	15	34.8 ± 1.9	525	1042.7	4.1	2.0 (n=30)
				Mosimane	1836	12	29.5 ± 1.8	372	1150.3	4.9	3.3 (n=39)
				Other-tree	14 115	49	35.1 ± 3.0	1720	1932	8.2	1.1 (n=55)
Hwange National Park, Zimbabwe	15 000	Closed woodland with dense shrubs	Deep Kalahari sandy soils and basalt clays	Main camp	1463	12	19.4 ± 10.3	209.7	970	6.98	6.3 (n=82)
Venetia-Limpopo Nature Reserve, South Africa	330	Closed woodland with dense shrubs	Granites and sedimentary – sandy soils	Venetia	300	7	35.1 ± 3.0	56.2	614.3	5.3	2.5 (n=14)
Laikipia District, Kenya	10 000	Semi-arid rangelands and shrubby grassland	Clay and sandy soils	El Karama	48	4	28.6 ± 1.8	109.9	114.4	0.44	4.0 (n=4)
				Mugie	89	3	28.6 ± 1.8	84.1	85.8	1.05	3.0 (n=3)
				Mpala	170	3	21.7 ± 4.5	48.9	65.1	3.5	3.0 (n=3)
Serengeti National Park, Tanzania	20 000	Open plains	Deep clay soils	Short-grass dry	1327	11	18.6 ± 3.2	205.2	205.2	6.5	1.0 (n=11)
				Short-grass wet	1327	4	16.7 ± 3.8	66.8	66.8	19.8	1.0 (n=4)
				Long-grass dry	873	22	17.1 ± 2.3	375.3	375.3	2.3	1.0 (n=22)
				Long-grass wet	873	6	18.7 ± 3.5	112.4	112.4	7.8	1.0 (n=6)

Where appropriate, estimates are followed by one standard error of the mean. The values in parentheses are the total number of transects surveyed irrespective of being repeated or not.

^aStander (1998).

Table 2 Mean average density (individuals 100 km⁻²) of the respective large carnivores

Study site	Cheetah		Leopard		Lion		Spotted hyaena		Brown hyaena	
	Density	Spoor	Density	Spoor	Density	Spoor	Density	Spoor	Density	Spoor
Tsumkwe					0.3					
Experimental			1.45							
Kaudum					1.45					
Dune-north	0.54 ^a	1.7	0.27 ^b	0.8	0.67	1.6	0.90 ^c	4.7	1.6	5.2
Dune-south	0.54 ^a	4.9	0.27 ^b	0.4	0.95	2.9	0.90 ^c	3.4	1.6	6.4
Mabuasehube		2.4		5.6	1.68	4.5		5.9		13.6
Sesatswe		5.6		4.0	1.35	5.5		4.0		9.7
Mosimane		4.7		2.6	2.20	7.2		13.3		14.0
Other-tree		3.4		3.0		4.8		5.2		8.4
Main camp	0.21	0.05	1.03	0.29	2.73	9.5	11.4	38.9		
Venetia					3.3	9.7				
El Karama					5.8	18.2				
Mugie					6.0	17.8				
Mpala					6.15	22.5				
Short-grass dry	2.26	1.0		1.0	7.0	1.5	30.0 ^d	35.6		
Short-grass wet	6.78	9.0		0	20.0	10.5	215.0 ^e	161.7		
Long-grass dry	9.16	1.6		0	24.28	16.5	40.0 ^d	77.0		
Long-grass wet	2.29	0.9		6.2	21.08	8.0	99.6 ^e	99.6		

Spoor density (number of fresh tracks 100 km⁻¹) of the large carnivores we surveyed at 15 study sites.

^aA.K. Knight (unpubl. data).

^bBothma *et al.* (1997).

^cMills (1990).

^dDurant, Hilborn & Croft (2002).

^eDurant *et al.* (2003).

Carnivore densities

Some published studies from which we collated information reported estimated carnivore densities (Table 2). We used data collated for radio-collared or known individuals to estimate densities in other cases (White & Shenk, 2001). For these, we calculated 95% minimum convex polygons (Burt, 1943) representing an individual's home range. We argued that the group (n_r) of each radio-collared individual r contributed to the total population (N_i) because their territory ($T_{n,r}$) will comprise an overlap ($T_{o,n,r}$) with the total study area (A_i). The actual population density (D_i) for a study area was then calculated as the sum of each of these contributions divided by the size of the study area. We thus defined:

$$D_i = \frac{\sum_r \frac{T_{o,n,r} n_r}{T_{n,r}}}{A_i}$$

Note that this derivation only holds when most groups had an individual fitted with a radio-collar.

The relationships between track and true carnivore densities

Typically, indices such as the number of tracks per unit distance or area may approach saturation at high densities. We explored these initially by plotting species- and substrate-specific track densities versus carnivore densities.

Saturation effects appeared to be evident only for high densities of spotted hyaena *Crocuta crocuta* on clay-soil substrates. We thus fitted an exponential association to the spotted hyaena data for clay-soils [$t_i = t_{\max}(1e^{-\alpha x_i})$, where t_i is the observed track index at site i , t_{\max} is the expected asymptote at which an index will be saturated, α is the rate of change towards a t_{\max} at a constant rate, x_i is the observed carnivore density at site i].

We also recognized through our exploratory analyses that substrates may affect relationships, but with the exception of spotted hyaenas on clay soils, high-density saturation effects are not evident because species tend to occur at lower densities. For these remaining species–substrate combinations we fitted simple linear models (t_i is the $\alpha x_i + \beta$ where t_i is the observed track index at site i , α is the rate of change, x_i is the observed carnivore density at site i , and β is the intercept converged onto zero when zero carnivore density should predict zero track density).

Our data did not allow a complete test of each species–substrate combination. For clay soils we fitted models for lions *Panthera leo* and cheetahs *Acinonyx jubatus* separately, and tested for differences between them using linear comparisons. Because there was no statistically significant difference between these two models (see 'Results'), they were combined for subsequent analyses.

For sandy soils, our data for cheetahs, leopards *Panthera pardus* and both hyaenas were sparse, and hence we fitted a linear model for lions only. Then, using ANOVA we tested whether the residuals predicted for lions, cheetahs, leopards

and both hyaenas differed when residuals for cheetah, leopard and hyaena track indices were calculated from the lion model. We assumed that the data can be described by a common model if these were not different, and therefore (see 'Results') combined all sandy soil data in one single linear model.

Sampling and precision

The ratio between the kilometres covered and the size of a study site (A_i) provided an index of 'sampling effort' ($E_{s,i} = A_i / \sum_{j=1}^n d_{i,j}$) where $d_{i,j}$ is the distance covered on a transect j of a total of n transects in area i (see Table 1). The repeated nature of our survey design, thus, includes both spatial (how many transects) and temporal (how many repeats) components of effort. Although this imperils assumptions of independence of samples, this is justified by the low encounter rate of tracks and the reasonable sampling intervals. Repeatedly sampling the same transect allows the recording of track incidences that is less influenced by random short-term effects of other factors on the encounter rate of tracks. This compromise affects the ability to derive confidence intervals for track densities, and hence carnivore densities. We thus measured the distance (km) between finding sets of tracks and fitted a non-linear decay model ($t_i = ad_{i-t}^{-b}$, where t_i is the track density at study site i , d_{i-t} is the mean distance between sets of tracks and a and b are constants). We reasoned that if we could estimate confidence intervals for d_{i-t} (see Stander, 1998), we could simulate confidence intervals for t_i , and hence for carnivore densities. Desired CVs (coefficient of variance) for distances between sets of tracks were arbitrarily set at 20%, which should require a minimum number of track incidences to be found.

To address this, we checked the effect of sampling intensity on the precision of distances recorded for lion data at three study sites by selecting two samples of sets of tracks randomly, increasing these progressively and calculating CVs for distances between each set of tracks (Grieg-Smith, 1957). To check if density affected the relationships, we log-transformed the data and compared the resulting linear formats. Clumping followed (see 'Results') after which we fitted a single non-linear decay model to the data ($CV[d_{i-t}] = an_i^{-b}$, where $CV[d_{i-t}]$ is the CV of the distance between track incidences, and n_i is the number of tracts encountered at study site i). We then plotted the total distance that had to be surveyed to obtain the minimum number of track incidences that would ensure $CV[d_{i-t}] < 20\%$ against carnivore density.

These results allowed us to propose guidelines for designing a track-based carnivore survey, estimating carnivore density and confidence intervals and predicting future requirements depending on information needs. From observed CVs of distances between tracking incidences, we simulated confidence intervals of carnivore densities recorded at our study sites. In this case, we randomly drew 10 000 distances between sets of tracks (d_{i-t}) from the

observed distribution defined by the mean distance between track incidences and $CV[d_{i-t}]$. For each distance, we predicted the track density using values for relationship parameters ($t_i = ad_{i-t}^{-b}$) based on point estimates and the standard error of a parameter. For each track density, we predicted the carnivore density using values for relationship parameters [$t_i = \alpha x_i + \beta$ or $t_i = t_{\max}(1e^{-\alpha x_i})$] based on point estimates and the standard error of a parameter. From these, we constructed a distribution of carnivore densities and extracted the confidence intervals from these for lions at selected study sites.

To evaluate needs if conservationists wish to detect changes of $\pm 10\%$ per annum, we used Gerrodette's (1987) inequality to check intervals of surveys required at the given CVs of population estimates that will have a power of 0.8 (i.e. conservationists have a 20% chance of concluding there is no trend when in fact there is). These serve as examples of how to use existing information to inform future surveys.

Results

Estimation of population densities

Estimated population densities of large carnivores in our data range from 0.54 to 215.00 individuals per 100 km² (Table 2). As most of these estimates came from long-term studies of radio-collared individuals, we do not provide confidence limits.

Track counts

In total, we surveyed 15 306.4 km of roads associated with 339 transects (Table 1). Survey efforts were variable across study areas and study sites. Estimates of track densities varied from 0.27 to 161.70 track incidences per 100 km (Table 2).

Relationship between large carnivore and track density

Track density could not be described satisfactorily by the true densities of felids using a single relationship ($t_i = 0.42x_i + 4.67$, $F_{1,22} = 5.71$, $P = 0.03$, $R^2 = 0.21$) with only 21% of variation accounted for and the intercept excluding zero (95% confidence interval of the intercept: 1.67–7.57). For spotted hyaenas, only two data points could be included for sandy soils so that data on clay soils may potentially bias conclusions about a general model.

For sandy soils, the lion density explained 97% of the range in the values of track densities ($t_i = 3.30x_i - 0.32$, $F_{1,8} = 279.90$, $P < 0.01$, $R^2 = 0.97$). The 95% confidence interval of the intercept included zero (95% CI: -2.01–1.37). The residuals for cheetah, leopard and hyaena track densities derived from the lion model did not differ from that of lion track densities ($F_{3,13} = 0.51$, $P = 0.68$). The combined model for all carnivore species on sandy soils described 96% of the variation in the data ($t_i = 3.15x_i + 0.40$, $F_{1,14} = 360.3$, $P < 0.01$, $R^2 = 0.96$, Fig. 1a)

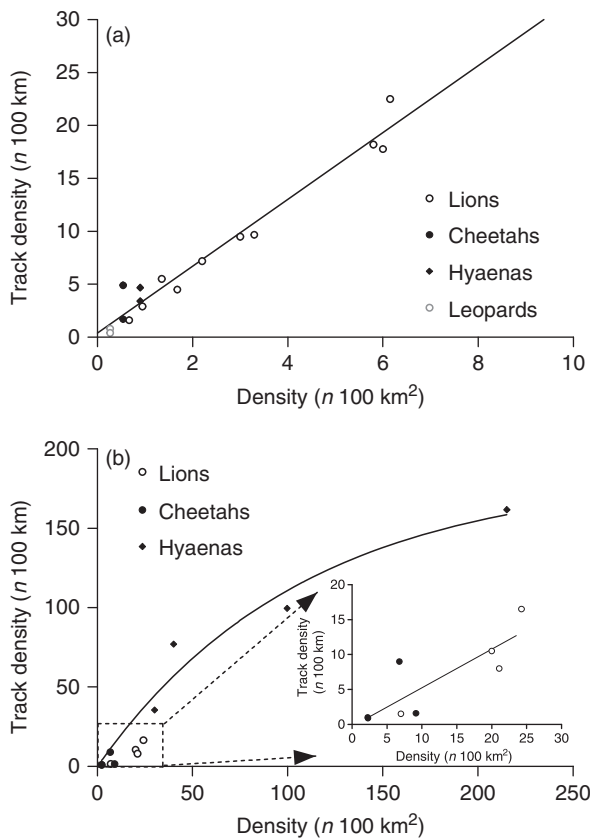


Figure 1 The relationships between known density ($n/100\text{km}^2$) and track density (tracks/100 km) in 12 study areas with sandy substrates (a) and four study area in clay-soil substrates (b) noted for lions *Panthera leo*, leopards *Panthera pardus*, cheetahs *Acinonyx jubatus* and spotted hyaenas *Crocuta crocuta*. Substrate as well as species influenced the relationships (see text).

and serves as a robust model to predict large carnivore densities from track densities on sandy soils.

For clay soils, we separated felids from hyaenids. Spotted hyaena track densities were exponentially associated with true densities in a true saturation model [$t_i = 183.60(1e^{-0.009x_i})$, $R^2 = 0.93$, $n = 4$, Fig. 1b]. Comparison of linear models for lions and cheetahs revealed no difference (slopes: $F_{1,5} = 0.57$, $P = 0.43$; intercepts: $F_{1,4} = 0.17$, $P = 0.70$) so that the combined felid model described 71% of the variation in the data ($t_i = 0.55x_i - 0.28$, $F_{1,6} = 14.69$, $P < 0.01$, $R^2 = 0.71$, Fig. 1b). The confidence interval of the intercept also included zero (95% CI: $-5.30-4.74$). Linear models differed for the estimation of large carnivore densities on sandy and clay soils (slopes: $F_{1,18} = 77.21$, $P < 0.01$).

Estimating survey needs

Track density declined non-linearly with the mean distance between track incidences ($t_i = 56.42d_{i-t}^{-0.66}$, estimated from log-transformed data linear regression, $F_{1,10} = 135.05$, $P < 0.01$, $R^2 = 0.94$, Fig. 2a). The coefficient of variance of

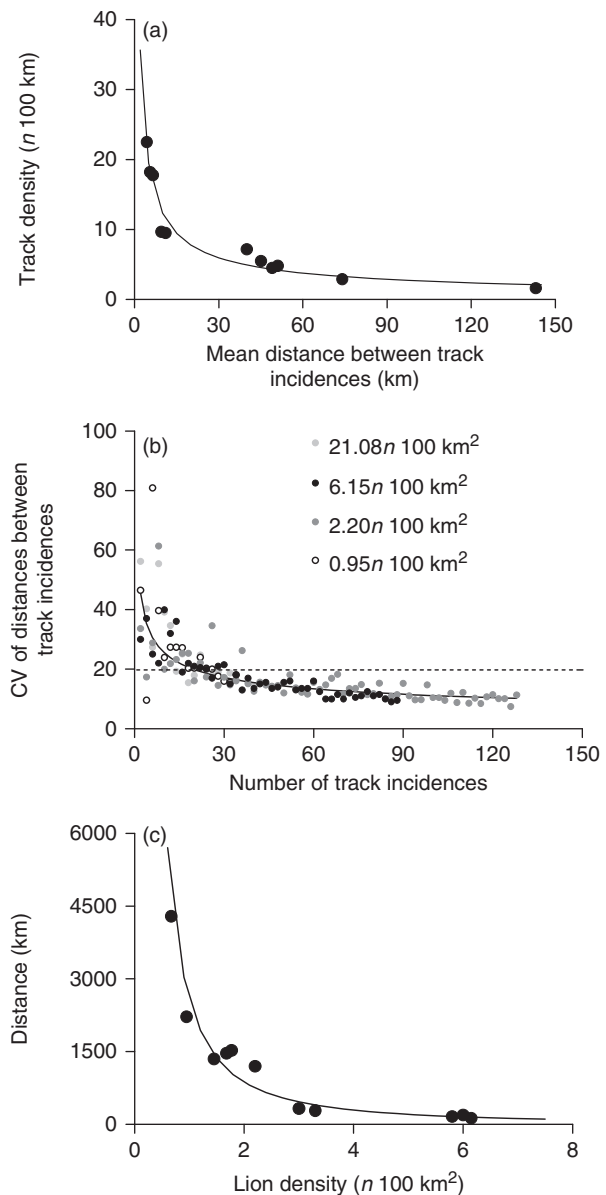


Figure 2 The relationships between survey features to assist defining the survey effort (distance) for expected densities. We illustrate lions *Panthera leo* as a case study. (a) Track densities declined exponentially as the distance between incidences of finding tracks increased. (b) The CVs of distances between finding incidences of tracks were not affected by density. Researchers need to find 30 tracks to ensure CVs of distances between track frequencies smaller than 20% (horizontal broken lines). (c) The distance required to find the appropriate number of track incidences declined as density increased.

distances between tracking incidences decreased with increasing sampling effort (Fig. 2b). The effect of sampling effort was the same for different densities and substrates (slopes: $F_{2,119} = 0.81$, $P = 0.44$; intercepts: $F_{2,121} = 0.74$, $P = 0.48$). We, thus, fitted a common model irrespective of density ($CV[d_{i-t}] = 58.33n_i^{-0.36}$, estimated from log-transformed data linear regression, $F_{1,123} = 238.90$, $P < 0.01$,

Table 3 Estimated lion *Panthera leo* densities (\hat{x}_i) and confidence intervals (95% CI) for sites where we had estimates of mean distance between track incidences (d_{t-i}) and the CVs of the mean distance between track incidences ($CV[d_{t-i}]$)

Study site	x_i	\hat{x}_i	95% CI	To detect 10% increase				To detect 10% decrease			
				<i>n</i>	Interval	Uncertainty	Risk	<i>n</i>	Interval	Uncertainty	Risk
Dune-north	0.67	0.38	0.36–0.40	2	1	1	10%	2	1	1	–10%
Dune-south	0.95	0.79	0.73–0.85	2	2	2	21%	2	2	2	–19%
Mabuasehube	1.68	1.30	1.23–1.36	2	1	1	10%	2	1	1	–10%
Sesatswe	1.35	1.62	1.52–1.71	2	1	1	10%	2	1	1	–10%
Mosimane	2.20	2.16	2.05–2.27	2	1	1	10%	2	1	1	–10%
Venetia	3.30	2.95	2.77–3.17	2	2	2	21%	2	2	2	–19%
Short grass wet	20.00	19.53	15–62–25.88	3	3	6	77%	3	3	6	–47%
Long-grass dry	24.28	30.41	26.38–35.99	2	3	3	33%	3	2	4	–34%
Long-grass wet	21.08	15.00	12–67–18.47	3	2	4	46%	3	2	4	–34%

We also provide the estimates (x_i) extracted through other methods for each study site *i* included. We provide intervals (years) needed to detect 10% increases and decreases, the time (years) it will take to detect a change (uncertainty), and the total amount of change by the time it is detected (risk) estimated using Gerrodette's (1987) inequality.

$R^2 = 0.66$, Fig. 2b). The model predicted that finding 19 track incidences should on average provide $CV[d_{t-i}] < 20\%$, but 30 incidences will most often ensure a $CV[d_{t-i}] < 20\%$. The distance (km) covered by the total amount of transects to encounter 30 track incidences on sandy soils decreased non-linearly with an increase in density ($D_i = 2579.90N_i^{-1.55}$, estimated from log-transformed data linear regression, $F_{1,9} = 156.58$, $P < 0.01$, $R^2 = 0.95$, Fig. 2c). We only had one estimate of distance to encounter 30 track incidences for clay soils. Our sandy soil model predicted 22.5 km, in stark contrast to 274.1 km surveyed in the long grass wet season at the Serengeti study area.

Estimating carnivore density confidence intervals

Using the relationships between track densities and distances between track incidences, as well as track densities and carnivore densities, we estimated densities as well as confidence intervals (Table 3) for lions at study sites where we had relevant data. Our estimates of lion density varied inconsistently with that estimated through other means. In only three of the nine cases, did our estimated confidence interval include point estimates of lion densities obtained through other measures. However, low densities predicted from track densities were associated with sites that also had low densities recorded through other means (Table 3).

Predicting change

The precision of carnivore estimates derived from spoor indices for the nine study sites affected a number of surveys and the interval between surveys to detect a change (Table 3). Most study sites had a high precision resulting in a 10% change detected with only two surveys 1 year apart. Those with less precise estimates required up to three surveys, but these needed to be up to 3 years apart. For these, the uncertainty was as high as 6 years of not knowing what the trend is in carnivore numbers. More importantly, for these

study sites a total change of up to 77% would have occurred once the change is detected (Table 3).

Discussion

Indices based on track counts can provide useful estimates of carnivore abundance. We found consistent relationships between track densities and the actual carnivore densities, having taken account of the substrate. A concern with such proxy measures is that the index may be saturated at high carnivore densities (Caughley, 1977), but in fact this was problematic for only one species-specific case in our analysis – that of the spotted hyaenas at very high densities (see Conroy, 1996). For all the other site–species combinations we analysed, track densities increased linearly with carnivore densities, enabling the index to be used to estimate abundance (Schwarz & Seber, 1999; Williams, Nichols & Conroy, 2002).

Furthermore, the linear relationships identified for different carnivore species were sufficiently similar that, at least for sandy substrates, a single model suffices, despite the undoubted variation in behavioural ecology. Stander's (1998) conclusion was that such indices should be treated as situation specific. Clearly, this conclusion is a prudent precautionary starting point, but our findings provide evidence of helpful generalization. A particular strength of our method is that it provides confidence intervals of the estimates. In the case of lions, only a third of the population estimates reported by other methods presented confidence limits.

There are several other methods available for estimating the abundance of cryptic, shy, low-density species such as carnivores (e.g. call-ups, camera traps, see Balme *et al.*, 2009). All have inherent assumptions and practical strengths and weaknesses. Some of these techniques if properly executed can be costly and time consuming to implement (e.g. Karanth & Nichols, 1998; Jackson *et al.*, 2006). Track surveys overcome some of these difficulties, particularly with respect to cost and thus repeatability. However, our analyses highlight two prerequisites for the successful use of

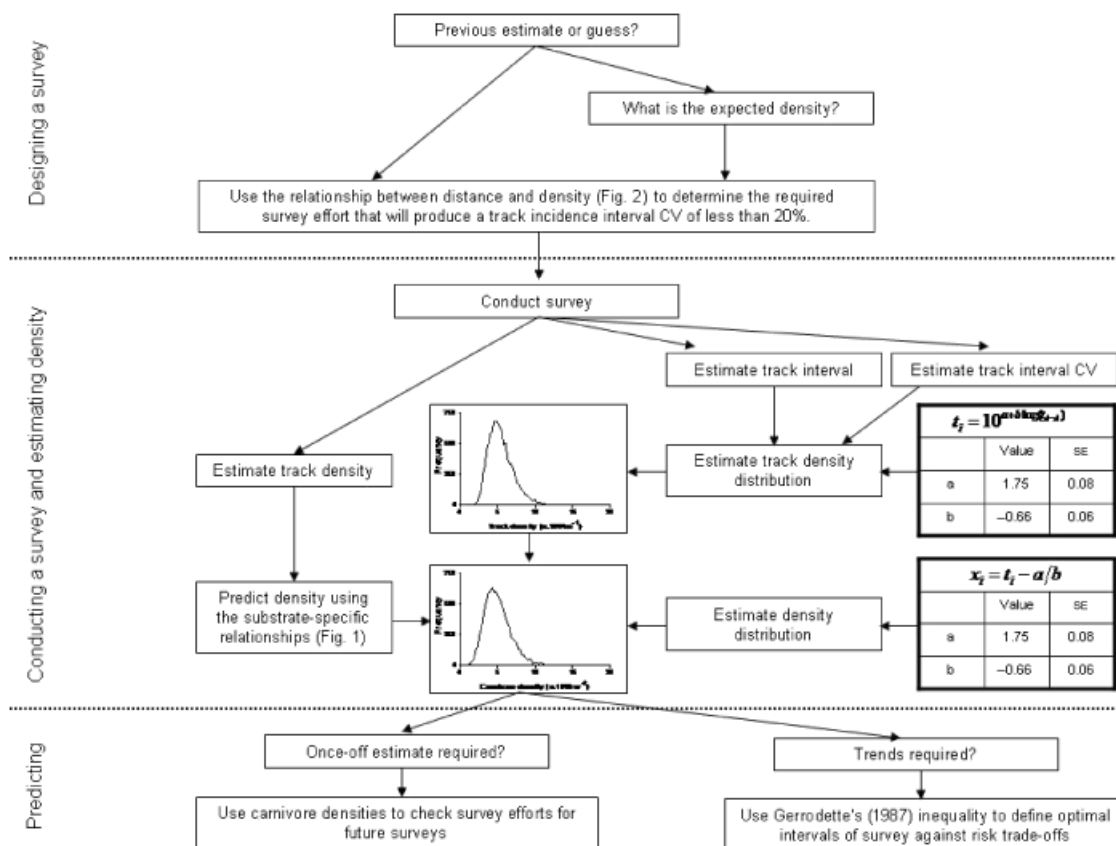


Figure 3 Flow diagram that guides conservationists wishing to estimate large carnivore densities and confidence intervals of these using track surveys. We provide the parameter estimates and standard errors of these for relationships between track density and distance between track incidences (Fig. 2a) as well as between track density and carnivore density (Fig. 1a). In our example, we made use of relationships established for sandy soils.

this track-based methodology, first suitable substrate and sufficiently skilled trackers and second, especially where the substrate is less suitable, the precautionary need to calibrate track density against known local carnivore density. Nonetheless, our results (Fig. 3) provide a generalized method for the estimation of large carnivore abundance. That this method allows for the calculation of confidence intervals is important to evaluate trade-offs for survey requirements that can inform management options.

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