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Evaluating Methods for Counting Cryptic Carnivores

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ABSTRACT Numerous techniques have been proposed to estimate carnivore abundance and density, but few have been validated against populations of known size. We used a density estimate established by intensive monitoring of a population of radiotagged leopards (*Panthera pardus*) with a detection probability of 1.0 to evaluate efficacy of track counts and camera-trap surveys as population estimators. We calculated densities from track counts using 2 methods and compared performance of 10 methods for calculating the effectively sampled area for camera-trapping data. Compared to our reference density (7.33 ± 0.44 leopards/100 km^2), camera-trapping generally produced more accurate but less precise estimates than did track counts. The most accurate result (6.97 ± 1.88 leopards/100 km^2) came from camera-trap data with a sampled area buffered by a boundary strip representing the mean maximum distance moved by leopards outside the survey area (MMDMOSA) established by telemetry. However, contrary to recent suggestions, the traditional method of using half the mean maximum distance moved from photographic recaptures did not result in gross overestimates of population density (6.56 ± 1.92 leopards/100 km^2) but rather displayed the next best performance after MMDMOSA. The only track-count method comparable to reference density employed a capture–recapture framework applied to data when individuals were identified from their tracks (6.45 ± 1.43 leopards/100 km^2) but the underlying assumptions of this technique limit more widespread application. Our results demonstrate that if applied correctly, camera-trap surveys represent the best balance of rigor and cost-effectiveness for estimating abundance and density of cryptic carnivore species that can be identified individually.
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Large terrestrial carnivores are notoriously difficult to monitor. Many species are shy, solitary, and nocturnal with wide ranging patterns and naturally low densities, confounding efforts to obtain reliable population estimates. Censuses or complete counts of carnivore numbers are often impractical, expensive, and time-consuming. As such, several alternative sampling measures have been developed to estimate abundance or provide indices of relative abundance (Schwarz and Seber 1999, Williams et al. 2002). Although most such methods attempt to employ a framework that is repeatable and objective, considerable conjecture remains over their theoretical applicability, and few have been tested in terms of accuracy or precision (Jennelle et al. 2002, Karanth et al. 2003).

Track counts have frequently been used to measure relative abundance of carnivore populations (Smallwood and Fitzhugh 1995, Beier and Cunningham 1996, Hayward et al. 2002). Although indices of abundance may be useful for specific management purposes, it is generally more desirable to establish absolute abundance (Bart et al. 2004). Indices are seldom equivalent in different habitats or consistent when applied over large geographic areas (Stephens et al. 2006). Furthermore, indices may not share a stable linear relationship with true abundance and can deviate at high or low population sizes (Conroy 1996). However, if a homogenous, proportional relationship can be reliably demonstrated, a correction factor may be used to convert the index to an estimate of abundance (Schwarz and Seber 1999, Williams et al. 2002). For example, Stander (1998) showed a strong linear correlation between true density of leopards (*Panthera pardus*) based on radiotelemetry data and track frequency. The resulting regression equation ($y = 1.9x$, where y is track density and x is true density) has been used in subsequent studies to calibrate track frequency data to true density (Funston et al. 2001, Gusset and Burgener 2005). It remains unclear, however, whether this equation's slope and intercept, and indeed, the relationship between true density and track frequency, remain constant under variable tracking conditions and changing leopard densities.

An alternative method of estimating population abundance from track counts is to use track frequency sampling in combination with closed capture–recapture models (Sharma et al. 2005, Choate et al. 2006), which assumes the identity of all individuals in the population can be determined with certainty from their tracks and that all individuals have an equal chance of being detected (Otis et al. 1978). Capture histories detailing track encounter rates within a limited sampling period can be used to estimate detection probabilities and population size. This approach has yet to be verified except in controlled situations with small numbers of known animals and remains to be rigorously tested under field conditions (Sharma et al. 2005).

Camera-trapping also uses capture–recapture sampling to estimate population size. Karanth and Nichols (1998) first developed this method to monitor tiger (*Panthera tigris*) populations in India and it has since been used to estimate abundance in a range of other felid species that are individually identifiable (Henschel 2001, Trolle and Kerry 2003, Silver et al. 2004, Heilbrun et al. 2006, Jackson et al. 2006). Although the principles underlying camera-trap surveys are statistically robust, few studies have validated their results against independent abundance estimates. Ideally, such a comparison would be made where a population can be completely enumerated but that typically

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presents formidable practical challenges and has not yet been undertaken. Further, when providing a density estimate, size of the sampled area must be determined as precisely as possible (Karanth and Nichols 2002). Size of the sampled area is not necessarily equal to the area enclosed by the outer traps because home ranges of some individuals may extend beyond the borders of the survey area (Wilson and Anderson 1985). It is therefore customary to add a boundary strip onto the survey area. Karanth and Nichols (1998) used a boundary strip equivalent to half the mean maximum distance moved (HMMDM) by tigers photographed on >1 occasion as a proxy of home range radius. Subsequently, numerous authors have suggested that using HMMDM from photographic recaptures underestimates actual distances moved and thus overestimates the resulting population density estimates. Dillon (2005), Di Bitetti et al. (2006), and Soisalo and Cavalcanti (2006) proposed that a boundary strip calibrated using independent estimates of home range size obtained from radiotelemetry data would be more appropriate. Given the increasing use of camera-trap surveys, it is essential that these issues are addressed.

We used a complete count of radiocollared leopards to evaluate efficacy of track counts and camera-trap surveys as estimators of population abundance and density. We assessed accuracy, precision, and costs associated with each method to determine which is the most suitable for surveying individually identifiable cryptic carnivores.

STUDY AREA

The study occurred in the 210-km^2 Phinda Private Game Reserve (hereafter Phinda) in the Maputaland region of KwaZulu-Natal, South Africa (detailed description in Balme et al. 2007). The climate was warm to hot, humid subtropical with average annual rainfall of 550 mm and mean monthly temperatures ranging from 33° C in January to 19° C in July (Schultz 1965). The site was located within Natal lowveld bushveld, coastal, and bushveld–grassland vegetation zones (Low and Rebelo 1996). Phinda's primary use was as a high-end ecotourism destination, with 7 lodges and 124 beds for tourists.

METHODS

As part of an ongoing ecological study on leopards, we captured 35 individuals in Phinda between April 2002 and December 2007 and fitted each with a very high frequency radiocollar weighing approximately 250 g (Sirtrack Ltd., Havelock North, New Zealand; Balme et al. 2007). Since January 2004, between 10 and 15 individuals wore radiocollars at any one time. Although the study is ongoing and the number of animals with collars at any given time fluctuates due to deaths and newly captured animals, data we present here are from 2005 when we also conducted track counts and a camera-trap survey.

Twice daily, tourists were taken on wildlife-viewing game drives by highly trained guides who were skilled in tracking and locating sought-after species, including leopards. As part of their standard procedure, guides reported all sightings of leopards to us as they occurred via 2-way radios. We collected standard information from each sighting such as location, time, sex, and, importantly, whether the animal was radiocollared. Accordingly, guides acted as an important source of information on presence of new, uncollared animals in the population. We responded to all sightings in which a collar was not confirmed and attempted to capture the individual for radiocollaring.

Calculation of Reference Population Density

We estimated density of the radiocollared leopard population on Phinda using our telemetry data and a method described by White and Shenk (2001). We attempted to locate every leopard once daily and recorded its location to the nearest 50 m using a handheld Global Positioning System receiver or by radiotriangulation when a close approach was not possible. We calculated daily locations inside the study area as a proportion of the total number of locations for 4 3-month sampling periods (called quarters) during 2005 (Jan–Mar, Apr–Jun, Jul–Sep, Oct–Dec). We multiplied that figure by the number of individuals with collars during that quarter to obtain an abundance estimate for each. We calculated mean density (hereafter, reference density) by dividing the abundance estimate by the size of the study area.

Track Counts

We conducted track counts over a 130-km^2 area of the study site where sandy soils provided a suitable substrate for tracking; we excluded the mountainous southern portion of the reserve where it was impossible to reliably detect tracks on rocky substrate. We selected 4 transect routes ($\bar{x}$ distance $= 34.8 \pm 1.8$ km) that we sampled at equal frequency and which traversed all major vegetation types. We drove transects in the early morning at a constant 10–15 km/hour with a skilled observer seated on the front of the vehicle. For all fresh ($\leq$24 hr old) leopard tracks, we recorded identity and number of individuals present. We counted each individual's track once per road count and only used data from radiocollared individuals in all analyses. We established identity from tracks based chiefly on our knowledge of individuals' spatial patterns from telemetry. Firstly, we calculated the boundaries of core areas for each leopard, wherein that individual maintained sole use to the exclusion of other individuals of the same sex (G. A. Balme and L. T. B. Hunter, Panthera, unpublished data). Because of our monitoring intensity, we usually assigned tracks in core areas to the resident without ambiguity. In areas where neighboring home ranges overlapped, we were more conservative. We assigned identity based on animals' movements during the previous night (which we knew from nightly radiotracking), by unique identifying marks in the tracks of a few individuals, and by confirming the nearest animal to each track set by telemetry. To test our accuracy, we followed tracks after assigning identity on 23 occasions, confirming their identity each time. Where we could not confidently assign identification after this process, we excluded those tracks from analysis ($n = 4$). Although our method cannot provide absolute certainty with regard to correct identification of individuals from tracks, we believe the intensity of our capture and monitoring effort, combined with very limited evidence of uncollared animals in the population (see Results) provided a high degree of confidence.

Following Stander (1998), we defined track density as the number of individual tracks per 100 km and track frequency as the number of kilometers per leopard track. We estimated desirable sampling intensity in terms of a trade-off between effort and precision using bootstrap analyses (Sokal and Rohlf 1995). We randomly selected 2 samples and calculated mean and coefficient of variation. We then progressively increased number of samples to 4, 6, 8, . . ., calculating fresh means and coefficient of variation each time (Grieg-Smith 1957). We plotted these data against sampling effort (no. km driven) and arbitrarily determined sampling intensity at the point where the coefficient of variation reached an asymptote and did not markedly improve with an increase in sample size (Stander 1998).

We estimated density from track count data using Stander's (1998) calibration equation. We also assessed the relationship between our reference density and track density. We randomly selected an individual leopard and plotted the proportion of its recorded locations inside the sample area against the frequency distribution of that individual's tracks (Stander 1998). We repeated this procedure 3 times by increasing the sample size (no. of individual leopards) but following a sample and remove technique to ensure independence. We used the resulting regression equation (the Phinda calibration) to calibrate track density to absolute density and compared these results to estimates calculated using Stander's (1998) equation and our reference density.

We used track frequency data from 20 road counts (from a total of 36) conducted over the same quarter as our camera-trap survey to estimate population abundance and density using closed capture–recapture models (Otis et al. 1978). Each road count represented one sampling occasion and we developed capture histories for each radiocollared leopard based on whether we located its track. We analyzed the data using Program CAPTURE (Rexstad and Burnham 1991) and used the model selection function to determine which model and estimator best fit the data. We then computed detection probabilities for individual leopards and an estimate of population size and corresponding standard error. We tested the data for population closure in CAPTURE.

We calculated the width of the boundary strip by using HMMDM for individuals whose tracks were recorded on >1 occasion using the point at which we first located tracks as the reference point for the distance calculation. We added this boundary strip to the area delineated by the outermost roads driven during track counts to determine the effectively sampled area. We compared the resulting density estimate to reference density in the first quarter (Jan–Mar) when we conducted the 20 transects.

Camera-Trap Survey

We conducted a camera-trap survey from 3 January 2005 to 28 March 2005 by dividing the study area into 2 contiguous subsections and sampling each subsection for 40 days. Total number of captures for occasion 1 was the sum of captures occurring on the first day of trapping in each subsection, number of captures or recaptures for capture occasion 2 was the sum of captures or recaptures for the second day of each subsection, and so on (Karanth and Nichols 2002). To satisfy the closure requirement, we defined a sampling occasion as 2 successive trap nights, resulting in 20 sampling occasions for the entire 80-day survey. Without this compression, closure was not satisfied and only produced 7 additional captures and no additional individuals.

We placed camera stations to maximize leopard captures, usually on roads, trails, or game paths, but also in gaps where there was no evidence of leopards to satisfy the assumption that no animal had zero probability of being photographed. The smallest annual home range recorded for a leopard in Phinda was 14 km^2 for a newly independent subadult female (G. A. Balme and L. T. B. Hunter, unpublished data). We placed camera-traps $\leq$2 km apart, meaning that each theoretical minimum home range of 14 km^2 contained $\geq$2 camera stations.

We used 15 stations (30 cameras) in each subsection. Each station comprised 2 print cameras (DeerCam, Park Falls, WI) to simultaneously photograph both flanks of leopards. We loaded cameras with 36-print, 200 or 400 American Standards Association (ASA) 35-mm film; cameras were active around the clock, except for a 5-minute delay between pictures to avoid large herds of ungulates, exhausting film. We mounted cameras on trees or on wooden posts 2–3 m from the center of the trail or road at 20–40 cm above the ground. We checked each camera every 4 days to replace film and batteries. We identified individual leopards from photographs using variations in their pelage patterns. We compiled capture histories for all radiocollared individuals photographed and calculated the probability of capture per occasion and estimated population size in CAPTURE.

We used 5 methods of calculating buffer width to estimate the size of the effectively sampled area: 1) mean maximum distance moved by individuals outside the area delineated by the outer traps (MMDMOSA) during the survey period as determined from radiotelemetry data, 2) HMMDM by individuals photographed on >1 occasion, 3) HMMDM calculated from telemetry data during the 3-month survey period, 4) mean annual home range radius (95% min. convex polygon) of leopards for 2005, and 5) mean home range radius for the 3-month survey period. We calculated home range radius for a circle equivalent in area to the mean home range estimate by applying $A = \pi r^2$, where A is the estimated area of the mean leopard home range and r is the resultant buffer width. We calculated the effectively sampled area in 2 ways: 1) by adding the buffer width as a boundary strip to the minimum convex polygon defined by the outer traps (Karanth and Nichols 1998) and 2) by adding the buffer width as a circular band around each individual camera station (Silver et al. 2004). For clarity, we refer to them as boundary strip buffer and individual camera buffer, respectively. We calculated the effectively sampled

Table 1. Reference population density of leopards (no. of leopards/100 km^2) using Phinda Private Game Reserve, KwaZulu-Natal, South Africa, estimated from radiotelemetry data for 4 sampling periods in 2005.

Population variables	Jan–Mar	Apr–Jun	Jul–Sept	Oct–Dec	Annual total
No. of radiocollared leopards using study area	12	12	14	12	14
% locations within study area	75	80	76	66	66
Population abundance	8.96	9.61	10.64	7.97	9.29
Mean density	7.07	7.58	8.39	6.28	7.33

area for each possible combination in ArcView 3.2 with the Spatial Analyst extension and generated density estimates for each effectively sampled area. We evaluated these estimates against reference density from the first quarter (Jan–Mar), when we conducted the camera-trap survey. We calculated variance as described by Karanth and Nichols (1998).

Cost Comparisons

We calculated expenses specific to each sampling method, including both equipment and running costs, although we omitted general project expenses (e.g., cost of vehicles, accommodation). We calculated total time expended on each sampling method from daily records of time in the field (G. A. Balme and L. T. B. Hunter, unpublished data). We generally conducted each task (i.e., track counts, monitoring camera-traps, and radiotracking) separately so there was little overlap in expenditure per method.

We calculated all analyses and statistical comparisons using SPSS 11.5 (SPSS Inc., Chicago, IL). We measured significance at $P < 0.05$ and 2-tailed. We tested all variables for normality and used non-parametric tests where we could not normalize data. We give means with standard error as a measure of precision. We estimated approximate 95% confidence intervals by $\bar{x} \pm 1.96$ standard error ($\bar{x}$).

RESULTS

Calculation of Reference Population Density

In 2005, 14 radiotagged leopards used Phinda (Table 1). We located leopards inside the study area for 66% of all radiofixes (individual range: 23–100%), resulting in a mean annual density of 7.33 ± 0.44 leopards/100 km^2. Proportion of time leopards spent on Phinda among the 4 quarters was similar (Kruskal–Wallis Test: $\chi^2_3 = 2.401$, $P = 0.493$). The population reached its highest density (8.39 leopards/100 km^2) in the third quarter (Jul–Sep) when 2 subadults became independent and were radiocollared at 1 year old. One of these subadults was killed by lions in November and another adult male was shot on a neighboring property in October. Apart from these 2 individuals, no radiocollared leopards entered or left the population during 2005.

We knew of only one additional uncollared leopard on Phinda, an adult female who spent little time on the reserve as judged by our observations, camera-trapping, tracks, and reports from lodge guides (Table 2). We attempted but failed to capture her. We found no evidence of any other leopards occupying the study site from any method or during daily observations of radiotagged individuals.

Track Counts

We surveyed 1,253 km of road associated with 36 transects and counted 76 track sets from 9 radiotagged leopards. We also observed tracks we believed to be of the uncollared female leopard mentioned above on 6 occasions but omitted these from all analyses. We found more male leopard tracks ($n = 47$) on roads than would be expected from their relative abundance ($\chi^2_1 = 4.015$, $P = 0.045$).

We calculated track density to be 6.07 ± 0.24 leopard tracks/100 km and track frequency as one leopard track for every 16.49 ± 0.32 km of road driven. Precision, as measured by the coefficient of variation, increased dramatically in the first 200 km driven, reaching an asymptote at approximately 600 km (Fig. 1). Although the coefficient of variation continued to decrease, an increase in precision of only 2.3% was gained between 600 km and 1,253 km.

The relationship between track density and true density was linear but not significant ($y = 1.33x + 0.05$; $F_{1,2} = 6.587$, $P = 0.124$, $R^2 = 0.767$; Fig. 2). Although the regression was not significantly different to Stander's ($F_{1,6} = 0.923$, $P = 0.391$) and the intercepts were similar, estimated population density calculated using the Phinda calibration was 42% higher than that using Stander's (Table 3).

We identified tracks of 6 radiocollared leopards on 39 occasions during our camera-trap survey. Track capture frequencies ranged from 2 to 10 captures per individual ($\bar{x} = 6.50 \pm 1.38$). Program CAPTURE identified 2 models as appropriate for our data: M_o, which assumes equal capture probabilities for all individuals on all trapping occasions, and M_h, which allows for heterogeneous capture probabilities among individuals but assumes that capture probabilities are not affected by trap response nor do they vary over time (Otis et al. 1978). We chose to use the jackknife estimator associated with M_h, because the null estimator of M_o is known to be sensitive to violations of the underlying assumption of homogeneous capture probabilities (Karanth and Nichols 1998).

Program CAPTURE estimated a population of 6 ± 0.23 leopards with a capture probability per occasion of 0.33. Population closure was confirmed by CAPTURE ($Z = -0.325$, $P = 0.364$). Mean maximum distance moved by leopards was 3.63 ± 1.19 km, yielding an effectively sampled area of 93 km^2 and an estimated population density of 6.45 ± 1.43 leopards/100 km^2 (Table 3).

Camera-Trap Survey

Our sampling effort comprised 2,400 camera-trap nights (30 traps × 40 days × 2 blocks) and yielded photographs of 12 radiotagged leopards captured on 38 occasions. We excluded

Table 2. Time expended searching and number of collared and uncollared leopards seen by guides on Phinda Private Game Reserve, KwaZulu-Natal, South Africa, in 2005.

Month	Guide effort[a] (hr)	No. of leopard sightings	No. of individuals recorded	No. of uncollared individuals recorded
Jan	3,032	5	3	0
Feb	3,331	7	4	0
Mar	3,160	8	4	0
Apr	3,630	12	6	0
May	3,459	14	4	0
Jun	3,800	17	6	1
Jul	3,758	12	4	0
Aug	3,843	15	5	1
Sep	3,544	11	4	0
Oct	3,416	6	2	0
Nov	3,416	8	3	0
Dec	3,459	5	3	0
Total	41,846	120	9	1

[a] Guide effort is the aggregate of the time spent searching each day by all guides summed for each month.

from analysis one photograph of the uncollared female, 2 photographs of one 4-month-old cub, and 3 photographs in which we were unable to identify the individual. Capture frequencies ranged from 1 to 7 captures per individual ($\bar{x} = 3.17 \pm 0.56$). Program CAPTURE selected M_h as the best-fitting model for the data. Estimated population size using the jackknife estimator was 14 $\pm$ 3.91 leopards with a capture probability per occasion of 0.14. Population closure was confirmed by CAPTURE ($Z = 0.087$, $P = 0.535$).

Area of the polygon delineated by the outer camera-traps was 142.27 km^2. Mean annual home range size for 2005 for both male and female leopards combined was 35.75 $\pm$ 8.17 km^2 ($n = 14$, 95% min. convex polygon) yielding a buffer width of 3.37 km. Mean home range for the 12 photographed leopards over the quarter in which the camera-trap survey took place was 27.19 $\pm$ 8.50 km^2, yielding a buffer width of 2.94 km. Both the size of the effectively sampled areas ($t_3 = 20.509$, $P \leq 0.001$) and the estimated densities ($t_3 = -3.919$, $P = 0.030$) were larger when using the boundary strip buffer technique than when using the individual camera buffer technique (Table 4).

Comparison of Density Estimates

All density estimates were lower than the reference population density. The least accurate result came from using Stander's (1998) calibration to convert track frequency data to true density, where estimated density was <50 % of reference density. The Phinda calibration produced a better result but was nevertheless a considerable underestimate. The only track count estimate comparable to reference density arose when employing a capture–recapture framework applied to data when we identified individuals from their tracks.

We produced the most accurate result from camera-trap data with a boundary strip calculated using MMDMOSA combined with the individual camera buffer method to determine the effectively sampled area. In general, the individual camera buffer method performed better than the boundary strip buffer method, with reference density falling within the 95% confidence intervals for 4 of the 5 estimators. The only case in which this did not occur was when we calculated buffer width using HMMDM from telemetry data. In contrast, the reference density fell within the 95% confidence intervals for only 2 of the 5 estimators

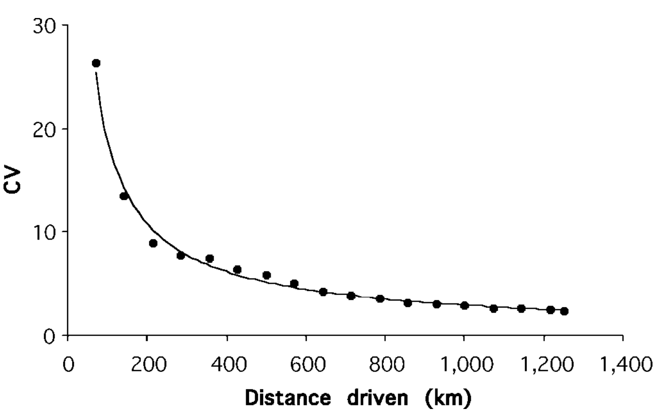

Figure 1. Relationship between sampling precision, measured by the coefficient of variation, and distance driven during track counts of leopards conducted in Phinda Private Game Reserve, KwaZulu-Natal, South Africa, 2005.

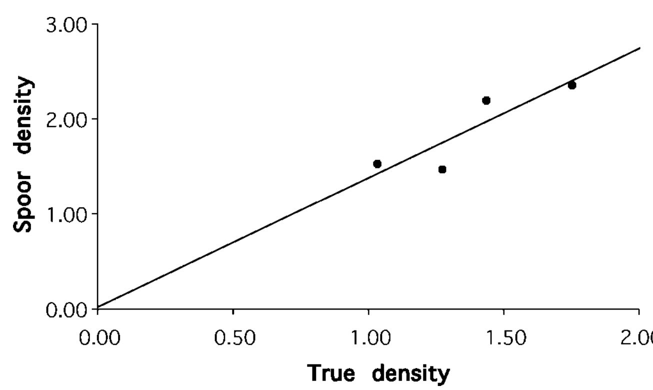

Figure 2. Relationship between reference density of leopards (no. of leopards/100 km^2), as determined from radiotelemetry data, and track density of leopards (no. of leopard tracks/100 km of road driven) in Phinda Private Game Reserve, KwaZulu-Natal, South Africa, 2005. Data points represent 4 independent comparisons resulting from the sample-and-remove technique.

Table 3. Estimated population densities of leopards (no. of leopards/100 km^2) in Phinda Private Game Reserve, KwaZulu-Natal, South Africa, derived from track counts in 2005.

Method	D[a] $\bar{x}$	SE	CI[b]	PRB[c]
Stander (1998) calibration	3.19	0.13	2.94–3.44	−55
Phinda calibration	4.53	0.18	4.18–4.88	−36
Capture–recapture	6.45	1.43	3.67–9.23[d]	−9

[a] Estimated population density.
[b] The 95% CI for density estimates.
[c] % relative bias calculated by $[(D-d)/d] \times 100$ where D is estimated density and d is reference density.
[d] Density falls within the estimated CI.

using the boundary strip buffer method, namely when we used MMDMOSA and HMMDM from photographic recaptures to calculate buffer width. Precision, as measured by the coefficient of variation, was lower for camera-trapping methods ($\bar{x} = 0.28 \pm 0.01$) than for estimates derived from track counts ($\bar{x} = 0.10 \pm 0.06$).

DISCUSSION

The intensity of our capture and monitoring effort, combined with ancillary measures of leopard presence, ensured that most of the leopard population using Phinda was known. However, because our chief objective was to evaluate methods rather than to establish actual density of our study population, we only used data from radiocollared individuals in all population metric analyses. In this way, we were certain that our reference population had a detection probability of 1.0 (Williams et al. 2002), providing the most rigorous comparison between population estimation methods.

Stander's (1998) calibration technique of using track frequency to estimate population density has been employed successfully only in semiarid environments where carnivore densities are low and tracking conditions ideal. Our results suggest that at higher densities and with variable tracking substrates, accuracy levels are diminished and Stander's (1998) method has limited applicability. The underestimates in Phinda and the nonsignificant relationship between track density and reference density highlights some of the challenges in applying the technique. Sampling heterogeneous landscape poses a problem because carnivores frequent certain habitat types at higher than expected frequencies (Van Dyke et al. 1986, Smallwood and Fitzhugh 1995, Balme et al. 2007). Changing substrates could also have affected the frequency at which we detected tracks. Soils in sand forest and closed red sand bushveld were better for track deposition than soils in open red sand bushveld and open mixed bushveld, but leopards showed preference for hunting in the latter 2 habitats (Balme et al. 2007). Finally, variation between individual animals may affect track detection frequencies; for example, male leopards used roads more regularly than did females. Additionally, leopards are protected in Phinda and might show high levels of road use compared to less-secure populations. Leopard activity in Kaeng Krachan National Park, Thailand, was lower in areas near the park's entrance road than in areas away from roads (Ngoprasert et al. 2007). All of these factors influence the relationship between track density and true density and therefore utility of the method.

Using a capture–recapture framework on track count data produced a more accurate result but, in application, relies upon numerous questionable assumptions. Most important is the ability to distinguish individual animals from their tracks. We achieved this by an intensive capture and monitoring effort of leopards that yielded very detailed knowledge of their spatiotemporal patterns. Most carnivore studies lack this capacity and rely on other techniques that

Table 4. Population densities of leopards (no. of leopards/100 km^2) in Phinda Private Game Reserve, KwaZulu-Natal, South Africa, estimated from a camera-trap survey in 2005.

		Boundary strip buffer (Karanth and Nichols 1998)					Individual camera buffer (Silver et al. 2004)				
			D[b]					D[b]			
Method of buffering	Buffer width	Â(W)[a]	$\bar{x}$	SE	CI[c]	PRB[d]	Â(W)[a]	$\bar{x}$	SE	CI[c]	PRB[d]
MMDMOSA[e]	2.05	270	5.19	1.41	2.43–7.95[f]	−27	201	6.97	1.88	3.29–10.65[f]	−1
HMMDM (camera-traps)[g]	2.21	280	4.99	1.45	2.15–7.83[f]	−29	213	6.56	1.92	2.80–10.32[f]	−7
HMMDM (telemetry)[h]	4.12	425	3.29	0.95	1.43–5.15	−53	372	3.76	1.10	1.60–5.92	−47
Home range (full yr)[i]	3.37	366	3.83	1.09	1.69–5.97	−46	308	4.55	1.30	2.00–7.10[f]	−36
Home range (survey period)[j]	2.94	333	4.20	1.20	1.85–6.55	−41	273	5.13	1.48	2.23–8.03[f]	−27

[a] Effectively sampled area.
[b] Estimated population density.
[c] 95% CI for density estimates.
[d] % relative bias calculated by $[(D-d)/d] \times 100$ where D is estimated density and d is reference density.
[e] Mean max. distance moved by individual leopards outside the area delineated by the outer traps during the survey period as determined from radiotelemetry data.
[f] Density falls within the estimated CI.
[g] Half the mean max. distance moved by leopards photographed on >1 occasion.
[h] Half the mean max. distance moved by leopards calculated using telemetry data during the 3-month survey period.
[i] Mean annual home range radius (95% min. convex polygon) of leopards for 2005.
[j] Mean home range radius (95% min. convex polygon) of leopards for the 3-month survey period.

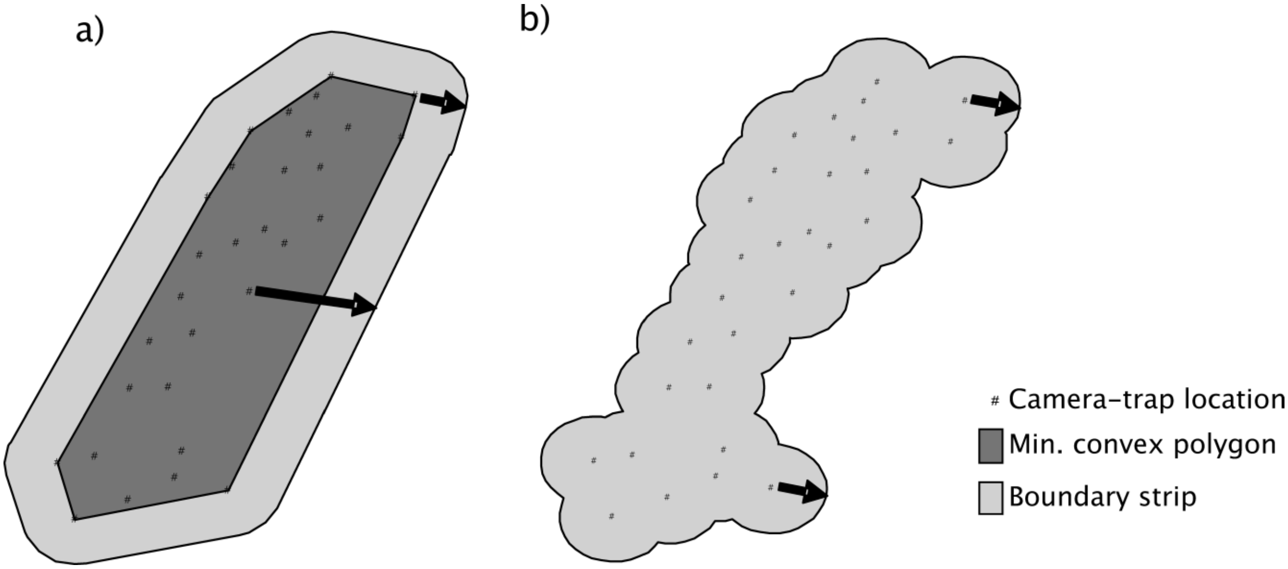

Figure 3. Representative survey areas for leopards in Phinda Private Game Reserve, KwaZulu-Natal, South Africa, 2005, demonstrating how distance between outlying camera-traps and the edge of the effectively sampled area varies for the a) boundary strip buffer method (Karanth and Nichols 1998) but remains constant for b) the individual camera buffer method (Silver et al. 2004). We calculated width of the boundary strip using half the mean maximum distance moved by leopards photographed on more than one occasion.

have their own limitations. Stander et al. (1997) showed that highly skilled Ju/'Hoan trackers in Namibia could reliably identify individual leopards, lions (*Panthera leo*), and wild dogs (*Lycaon pictus*) using gross footprint morphology in 98% of 569 track reconstructions. Broader application of this method is limited, however, in that it relies on highly skilled trackers working under optimal tracking conditions. Smallwood and Fitzhugh (1993) and Sharma et al. (2005) distinguished between small numbers of pumas (*Puma concolor*) and tigers, respectively, using discriminant function analyses applied to standardized pugmark measurements. Such a supervised classification system requires class assignments (i.e., individual identities) before analysis (Sokal and Rohlf 1995), which effectively defeats the purpose of surveying most candidate populations where little prior information is available. Riordan (1998) attempted to address this by using an unsupervised Bayesian classification method to distinguish between track sets from different individuals, but his study took place in a controlled situation with prepared substrates and small sample sizes, which would be difficult to replicate under field conditions. Regardless, shape discrimination–based identifications are, at best, probabilistic and consequently cannot be used in closed capture–recapture models (Karanth and Nichols 2002). Ulizio et al. (2006) overcame this by backtracking all individuals recorded in track counts until a hair or scat sample was obtained that was genetically discernable. Herzog et al. (2007) used unique papilla patterns on the underside of fisher (*Martes pennanti*) metacarpal pads to distinguish individuals (similar to human fingerprint analysis) from track-plate tracings and predicted likelihood of misidentifying an individual was 0.00003. Therefore, in exceptional circumstances, it may be possible to apply capture–recapture procedures on track frequency data, though most field-based scenarios will present tremendous challenges in ensuring all underlying assumptions are met.

The camera-trap survey generally produced more accurate but less precise results than track counts, which is probably a consequence of the small sample sizes likely to characterize camera-trap surveys of low-density, cryptic carnivores (Karanth and Nichols 2002). However, standard error of our estimated population size (3.91) and probability of capture per occasion (0.14) were comparable to other camera-trapping studies of large felids (Karanth and Nichols 1998, Silver et al. 2004, Karanth et al. 2004, Soisalo and Cavalcanti 2006). Our results indicated that the method we used to calculate buffer width, and hence the effectively sampled area, had a profound influence on accuracy of density estimates from capture–recapture data. The primary objective when estimating size of the boundary strip is to determine how far individuals move outside the sampled area during the survey period (Otis et al. 1978). Both the size and shape of the sampled area will influence the proportion of animals that have home ranges entirely contained within its boundaries versus those that overlap it to varying degrees (Parmenter et al. 2003). The marked difference in estimator performance between the individual camera buffer method and the boundary strip buffer method can be explained by the relative sensitivity of the 2 procedures to variations in the shape of the sampled area. Ideally, trapping grids should be uniform in shape with cameras evenly spaced throughout the sampled area (Karanth and Nichols 2002), which in reality is rarely possible. When using the individual camera method, distance from the edge of effectively sampled area to outlying cameras remains constant regardless of survey design (Fig. 3), which is not necessarily true of the boundary strip buffer method. The minimum convex polygon technique used to calculate the sampled area is extremely sensitive to irregularities in shape

Table 5. Cost comparison of survey methods we used to estimate leopard population density in Phinda Private Game Reserve, KwaZulu-Natal, South Africa, 2005.

Cost	Radiotelemetry Capture	Radiotelemetry Monitoring	Radiotelemetry Total	Track counts	Camera-trapping
Financial (US$)	13,512	8,800	22,312	490	4,749
Time (hr)	1,047	2,450	3,497	216	174

(Mohr 1947) and even if the actual area covered by cameras remains the same, size of the sampled area may vary dramatically. Furthermore, distance from outlying cameras to the boundary of the effectively sampled area can be highly variable within one survey (Fig. 3), which could potentially lead to inclusion of areas outside the range of captured individuals and is especially problematic when trapping grids are surrounded by land of patchy quality (Dillon 2005).

All 12 leopards we used in the camera-trap survey analyses were radiocollared, enabling us to determine MMDMOSA by telemetry. As expected, density estimates generated using MMDMOSA showed the lowest bias compared to reference density. However, contrary to recent suggestions (Dillon 2005, Di Bitetti et al. 2006, Soisalo and Cavalcanti 2006), the traditional method of using HMMDM from photographic recaptures did not result in gross overestimates of population density. Indeed, HMMDM displayed the next best performance after MMDMOSA in estimating reference density. We believe that the sample size of telemetered individuals is a key issue. Our study is the first to be able to rely on an intensive capture effort in which most of the population was collared, which has important implications for calculation of mean home range size for the sampled population and, therefore, of the buffer size as calculated by telemetry. In the case of earlier efforts, smaller sample sizes of telemetered animals and, perhaps more importantly, a much lower proportion of the population with radiocollars, likely yielded home range estimates that should not be applied to the entire population. Accordingly, their conclusions on the validity of using HMMDM for calculating the sampled area need to be treated with caution.

Choice of survey method is dependent on the objectives of the study and the resources available to carry out those objectives. Relative costs, in terms of both time and money, varied considerably among the 3 techniques (Table 5). Intensive radiotelemetry provided the greatest accuracy; however, it is prohibitively expensive if the desired result is solely to determine density. Our results demonstrate that if applied correctly, camera-trapping can produce similarly reliable estimates at a fraction of the cost. Although track counts are cheaper to conduct than camera-trap surveys and easier to implement across a larger area, accuracy levels are poor. Track counts may be satisfactory when the objective is simply to gauge trends in abundance over time. In our study, track counts yielded more precise results with a similar amount of effort and fewer costs. Even so, caution should be exercised when using relative abundance indices to make comparisons over space and time (Pollock et al. 2002), and we would still recommend calibrating the index with ≥1 other independent abundance estimate.

It is surprising that camera-trapping has not been more widely adopted by the statutory authorities responsible for conservation and management planning for carnivores. In the case of leopards, the prevailing view among management agencies holds that the species is too difficult or costly to count, even for potentially invasive management actions such as assigning trophy hunting quotas (Convention on International Trade in Species of Wild Fauna and Flora 2007). To date, the alternative for estimating leopard numbers for management decisions has mostly entailed guesswork or resorting to overly simplistic modeling techniques (Martin and de Meulenaer 1988, Norton 1990). As our comparison shows, camera-trap surveys offer the best balance of rigor and cost-effectiveness. Although readily used by wildlife biologists to monitor cryptic carnivores, the influence of camera-trapping in guiding management and setting policy remains disappointing (Karanth et al. 2003). As the first assessment of camera-trapping against a censused population of large cats, we hope our results will encourage wider adoption of the technique.

MANAGEMENT IMPLICATIONS

Establishing reliable population estimates of large carnivores is essential for effective conservation and management activities. Our data demonstrate utility and cost-effectiveness of camera-trap surveys for estimating cryptic carnivore numbers, even in small sample areas such as ours. However, as we show experimentally, varying the method for calculating the sampled area has a significant effect on the resulting density estimates and we recommend standardizing the technique with the application of the individual camera buffer method. Logistical constraints and poor performance of track counts limit their wider applicability, except perhaps in ideal circumstances where they may be suitable for monitoring trends in abundance at the same site over time.

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