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Abstract: 1. Carnivores can have critical impacts on ecosystems, provide economic value through tourism and are often important flagships. However, their biological traits (e.g. low density, cryptic colouration and behaviour) make them difficult to monitor and hence wildlife managers rarely have access to reliable information on population trends, and long-term information at the community level is almost completely lacking. 2. We use data from transect counts in the Serengeti ecosystem in Tanzania to examine trends in abundance for seven co-existing carnivore species. Distance-based transect counts between 2002 and 2005 are compared with adjusted data from fixed-width transect counts across the same area in 1977 and 1986. 3. Distance-based methods provided density indices for the seven most commonly seen carnivores: lion Panthera leo, spotted hyaena Crocuta crocuta, golden jackal Canis aureus, black-backed jackal Canis mesomelas, cheetah Acinonyx jubatus, side-striped jackal Canis audustis and bat-eared fox Otocyon megalotis. Detection curves were used to correct estimates fromearlier fixed-width transect counts. 4. Trend analyses detected significant declines in densities of golden and black-backed jackal and bat-eared fox, but found no significant changes in spotted hyaena, lion, cheetah and side-striped jackal. 5. Overall, despite wide confidence intervals, we show that distance-based data can be used effectively to detect long-term trends and provide critical information for conservation managers. Power analysis demonstrated that for the most frequently seen species, spotted hyaena, golden jackal and lion, abrupt declines of up to 20% may be detectable through long-term monitoring; however, for the remaining species, declines of 50%may only be detected half the time. 6. Synthesis and applications. Distance methods provide a tool for rapid counts and monitoring of several species of carnivores simultaneously in suitable habitats and can be combined with historical fixed-width transect counts to test for changes in density. The method can provide key information to managers on long-term population trends and sudden abrupt changes in population size across a carnivore community.

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Long-term trends in carnivore abundance using distance sampling in Serengeti National Park, Tanzania

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Summary

1. Carnivores can have critical impacts on ecosystems, provide economic value through tourism and are often important flagships. However, their biological traits (e.g. low density, cryptic colouration and behaviour) make them difficult to monitor and hence wildlife managers rarely have access to reliable information on population trends, and long-term information at the community level is almost completely lacking.

2. We use data from transect counts in the Serengeti ecosystem in Tanzania to examine trends in abundance for seven co-existing carnivore species. Distance-based transect counts between 2002 and 2005 are compared with adjusted data from fixed-width transect counts across the same area in 1977 and 1986.

3. Distance-based methods provided density indices for the seven most commonly seen carnivores: lion *Panthera leo,* spotted hyaena *Crocuta crocuta,* golden jackal *Canis aureus,* black-backed jackal *Canis mesomelas,* cheetah *Acinonyx jubatus,* side-striped jackal *Canis audustis* and bat-eared fox *Otocyon megalotis*. Detection curves were used to correct estimates from earlier fixed-width transect counts.

4. Trend analyses detected significant declines in densities of golden and black-backed jackal and bat-eared fox, but found no significant changes in spotted hyaena, lion, cheetah and side-striped jackal.

5. Overall, despite wide confidence intervals, we show that distance-based data can be used effectively to detect long-term trends and provide critical information for conservation managers. Power analysis demonstrated that for the most frequently seen species, spotted hyaena, golden jackal and lion, abrupt declines of up to 20% may be detectable through long-term monitoring; however, for the remaining species, declines of 50% may only be detected half the time.

6. *Synthesis and applications*. Distance methods provide a tool for rapid counts and monitoring of several species of carnivores simultaneously in suitable habitats and can be combined with historical fixed-width transect counts to test for changes in density. The method can provide key information to managers on long-term population trends and sudden abrupt changes in population size across a carnivore community.

Key-words: African lion, bat-eared fox, black-backed jackal, carnivore community, carnivore density, cheetah, golden jackal, monitoring, side-striped jackal, spotted hyaena

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Introduction

Carnivores play an important role in ecosystem function (Ginsberg 2001) and are often a major attraction for tourists (e.g. Okello, Manka & D'Amour 2008), and thus an important source of revenue for many protected areas (Balmford *et al.* 2009). However, despite their ecological and economic significance, there is surprisingly little information on long-term population trends of carnivore species in most protected areas. This is of particular concern as the position of carnivores at the top of the food chain and their often problematical relationships with humans and domestic animals make them especially vulnerable (Ginsberg 2001).

Carnivores have evolved to be effective killers, making them exceptionally susceptible to aggressive intraguild interactions (Palomares & Caro 1999). Interspecific predation, kleptoparasitism and competition are increasingly recognised to influence the composition of carnivore communities, and coexistence is often maintained through a combination of resource partitioning and anti-predator behaviours. Such interactions result in particularly complex relationships between species within a community of carnivores, with important consequences to population dynamics and coexistence (e.g. Laurenson 1994; Creel & Creel 1996; Durant 1998, 2000a,b; Creel, Spong & Creel 2001; Kamler *et al.* 2003).

Fewer than 15% of the world's carnivores have received serious long-term scientific study (Ginsberg 2001), and hence the impacts of interspecific interactions at the population level, the level of interest to wildlife managers, are poorly understood. Long-term monitoring of the carnivore guild is key to understanding quantitative relationships between members of the carnivore community and establishing the influence of interspecific competition on species diversity. Furthermore, long-term monitoring enables managers to assess relationships between changes in carnivore populations and their prey and detect unusual changes in density of one species over another, thus enabling interventions to maintain overall diversity. This information is particularly important, given that 32% of the world's 234 carnivore species are threatened (Sechrest *et al.* 2002).

Despite the importance of carnivore monitoring, there is little information on long-term trends across carnivore communities; existing information in Africa is largely limited to a handful of valuable long-term single species studies (e.g. Packer *et al.* 2005; Durant *et al.* 2007). This lack of information is due partly to difficulties in surveying carnivores, resulting from their biology, including extensive ranging patterns, low densities, cryptic habits, nocturnal movements and/or shy nature, often aggravated by persecution from humans. These characteristics make many traditional population survey methods impractical for counting carnivores; however, the development of distance sampling techniques has provided new opportunities (Buckland *et al.* 2001). Distance sampling techniques have been employed successfully for a variety of species in diverse ecosystems (see http://www.ruwpa.st-and.ac.uk/distancesamplingreferences/), but have rarely been used for carnivores. Despite this, the techniques are appropriate for carnivores, particularly medium to large species, provided habitats are relatively open and carnivores are reasonably well habituated, as in many well-visited protected savannas in eastern and southern Africa.

The Serengeti National Park is one of a handful of sites in Africa with a long-term monitoring programme of large herbivores (Campbell & Borner 1995). However, there is, at present, no established programme for carnivore monitoring. Carnivores on the Serengeti short and long grass plains were surveyed in 1977 and 1986 using fixed-width transects. In 2002/2003 and 2005, these surveys were repeated using distance-based methods, in order to

1. Establish whether the method can detect long-term trends in carnivore abundance and identify those species of carnivore appropriate to the method.

2. Establish a methodology to enable comparison between fixed-width transects and more recently implemented distance-based transects.

3. Combine with earlier surveys to identify long-term changes in density.

The results are used to develop recommendations for future surveys.

Materials and methods

THE SURVEY AREA

The survey area consisted of 2300–3000 km^2 in the southeast of Serengeti National Park (SNP) and northern and western portions of the Ngorongoro Conservation Area (NCA) (Fig. 1) (Serengeti Research Institute 1977a,b; Campbell & Borner 1986). The survey area was divided into two strata comprising LGP lying entirely within the SNP and short grass plains (SGP) located in the NCA and south and east SNP. Rain falls in a bimodal distribution and attracts migratory herbivores onto the SGP south and east of the survey area, after spending the long dry season in woodlands to the north and west (Sinclair & Arcese 1995). These herbivores are followed by non-territorial cheetah (Caro 1994) and commuting spotted hyaenas (Hofer & East 1995). Thus, numbers of hyaenas show a marked increase in the wet compared to dry season (Hofer & East 1995) when commuters greatly supplement residents. Numbers of cheetahs may also increase, as more cheetahs move onto the plains from surrounding areas (Durant *et al.* 1988). Lions shift their territories south and eastwards, moving from long grass to SGP (Schaller 1972). The other carnivore species in the survey area are all territorial and are not expected to move in response to migratory herds.

SURVEY METHODOLOGY

Previous fixed-width transect surveys are well documented (Serengeti Research Institute 1977a,b; Campbell & Borner 1986; Hofer & East 1995). They were conducted in May 1977, October 1977 and May 1986 and counted all carnivores within 100 m of the transect line (Fig. 1a).

Distance-based surveys were conducted in September 2002, May 2003, April 2005 and October 2005. A systematic set of parallel north–south transect lines were laid out 2 km apart over the same survey area, excluding a small special conservation area in the west (Fig. 1b). During surveys, closed 4WD vehicles with two co-operating observers (driver and passenger) were driven in straight lines

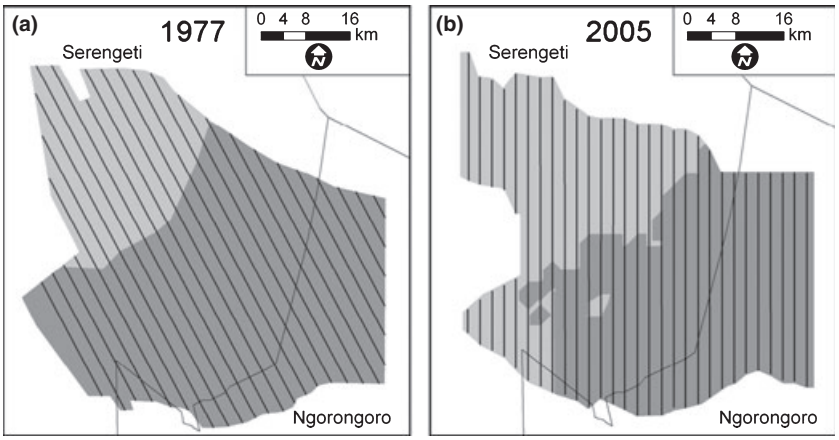

Fig. 1. Map of survey area (grey shading) and transects (parallel lines). (a) 1977 and 1986 surveys (transects from 1977 surveys are shown), (b) 2002/3 and 2005 surveys. A thin line denotes the border of Serengeti National Park and Ngorongoro Conservation Area. Light and dark grey shading denote the long (LGP) and short grass plain (SGP) habitat strata, respectively.

along pre-allocated transect lines. All carnivore groups (1 or more individuals) seen were recorded by species, number of individuals, location and time. The perpendicular distance of the centre of the group from transect line was estimated by eye according to cutpoints: 0, 10, 50, 100, 150, 200, 300, 400, 500 and > 500 m. Drivers maintained a steady speed that did not exceed 20 kph, and each survey took 3 days, including 1 day training in distance estimation by eye. Carnivores in the study area are habituated to vehicles.

LINE TRANSECT ANALYSIS

Distance data were analysed using conventional (CDS) and multiple covariate distance sampling (MCDS) (Buckland *et al.* 2001, 2004). Species' density, $\hat{D}$, was estimated from:

$$\hat{D} = \frac{n_c \hat{E}(c)}{2wL\hat{p}_c}. \qquad \text{eqn 1}$$

Where n_c is number of clusters (groups) detected and p_c probability of detecting a cluster within truncation distance w, $\hat{E}(c)$ expected cluster size and L total transect length. Calculations were performed in Distance 6.0 Release 2 (Thomas *et al.* 2010), except where noted.

Estimating probability of detection

Distance data were analysed in the same intervals used during surveys, with sighting distances for each species truncated as recommended by Buckland *et al.* (2001). Preliminary detection functions $g_c(x)$ were fitted to data, and the largest 0, 5 and 10% of distances removed, choosing the least amount of truncation which kept $g_c(w) > 0{\cdot}10$. This process suggested similar truncation distances at $w = 200$ m for all species except bat-eared fox; hence, for ease of comparison, all observations were truncated at this distance.

The uniform (U), half-normal (HN), and hazard-rate (HR) key functions were fitted to truncated data, with polynomial or cosine series expansion terms (Buckland *et al.* 2001). The Akaike Information Criterion (AIC) was used to choose between models. Rare species (< 60 clusters) were analysed jointly with species of similar size, with species as a covariate, and the detection function with lowest AIC selected. Species grouped in this way were spotted hyaena (52 kg; Kruuk 1972) and cheetah (39 kg; Caro 1994), and the canids – golden jackal, black-backed jackal, side-striped jackal and bat-eared fox (6, 7, 8 and 4 kg, respectively; Wayne *et al.* 1989; Maas & Macdonald 2004). For species with over 120 sightings (hyaena and golden jackal), we fitted separate detection functions by habitat (SGP or LGP), year and season (wet or dry), and used AIC for model selection. Final model fit was assessed using diagnostic plots and goodness-of-fit chi-square tests (Buckland *et al.* 2001). $\hat{p}_c$ was then calculated from

$$\int_0^w \hat{g}_c(x)dx/w \qquad \text{eqn 2}$$

Estimating average cluster size

For each species, log observed cluster size was regressed against estimated detection probability to test for 'size bias' (i.e. tendency to observe more large clusters at large distances). In all cases, the regression slope was not significantly different from zero ($P > 0{\cdot}15$), hence we used mean observed cluster size as an estimate of $\hat{E}(c)$. For species with > 60 observations, we modelled cluster size as a zero-truncated quasi-Poisson or negative binomial random variable fitted to a linear function of season, habitat and their interactions (Grogger & Carson 1991), using statistical software R 2.9.2 (http://www.r-project.org). In all cases, a model with pooled cluster size had a lower AIC, justifying use of pooled mean cluster size as an estimate of $\hat{E}(c)$ across years, habitats and seasons.

Density, abundance and variance estimation

We estimated density for each habitat stratum (LGP or SGP) within each survey where there was sufficient data (lions, spotted hyaenas and golden jackals), using eqn 1, and estimated abundance as density multiplied by stratum area. Estimates of encounter rate, $2n_c/wL$, were calculated separately for each stratum within each survey. Variances were estimated using the methods of Buckland *et al.* (2001), except for encounter rate variance, where estimator O2 was used to account for the systematic survey design as described and recommended by Fewster *et al.* (2009) and Fewster (2011). Variance in overall density across the survey area was calculated assuming that encounter rate estimates were independent between habitat strata and pooling estimates of $\hat{p}_c$ and $\hat{E}(c)$ across habitats (multipliers were required to achieve this in Distance).

FIXED-WIDTH TRANSECT ADJUSTMENT

We used information about detectability gained from distance-based transects to estimate detection probability for fixed-width surveys, where data were not partitioned into clusters. Hence, we calculated density from the probability of detecting individuals rather than clusters using:

$$\hat{D}_i = \frac{n_i}{2wL\hat{p}_i} \qquad \text{eqn 3}$$

where n_i is number of individuals detected and $\hat{p}_i$ is probability of detecting an individual within a strip of half-width $w = 100$ m.

$\hat{p}_i$ was calculated from eqn 2 with $w = 100$ after refitting the detection function using individual rather than cluster distances, assuming that detectability had not changed between surveys. Density was estimated using eqn 3, and calculations were conducted as for distance-based surveys.

ANALYSIS OF POPULATION CHANGE

Managers not only require information on long-term trends in population size, but also on sudden declines or increases, to enable mitigative responses. We therefore conducted two analyses to detect changes in population size for each species: (i) analysis to detect long-term trend increases or declines; (ii) abrupt change analysis to detect sudden changes in last wet/dry season survey. Long-term trends were assessed for each species using generalised linear models (GLMs) with number of detected individuals as the response variable and Poisson errors. Explanatory variables were year, season (dry/wet), habitat (SGP/LGP) and the interaction between season and habitat. Log effective area surveyed (transect length $\times$ $w\hat{p}$) was included as an offset term (see Hedley, Buckland & Borchers 2004). The year coefficient from the GLM was used to calculate percentage annual population growth rate r% (Gerrodette 1987).

The variance in trend calculated analytically by GLM underestimates true variance, as it does not incorporate error in estimation of the offset term, and transect counts are not strictly independent. We therefore used nonparametric bootstrap to estimate true variance in annual trends (Davison & Hinkley 2006). In each of 10 000 bootstrap replicates, we took a random sample of transect lines with replacement independently from each of the 1977, 1986, 2002/3 and 2005 survey sets. We re-fitted detection functions and GLMs and re-estimated the trend. We found no evidence of bias in the bootstrapped estimation of trend compared with the analytical estimate (sign test, $n = 7$, $P > 0{\cdot}1$). We calculated the bootstrap variance in trend and used lower 2·5th and upper 97·5th percentiles as 95% confidence intervals, making no assumptions about the underlying distribution. In one case (side-striped jackal), 17 of the 10 000 bootstrap replicates had too few data to fit the GLM, and these were removed before calculating variance and confidence intervals. The bootstrap analysis was performed in *R*, and detection functions were fitted using the MCDS analysis engine in distance. Investigations for abrupt recent change were performed using GLMs and bootstrapping as above, with an additional factor describing the most recent year versus all previous years.

COMPARISON WITH KNOWN LION AND CHEETAH DENSITIES

To test the validity of our results, we compared them with estimates of abundance of lions and cheetahs from two long-term projects within the survey area: the Serengeti Lion Project (SLP) and Serengeti Cheetah Project (SCP). The SLP provided estimates of total number of individually known lions alive at the end of the month of each survey in an approximately 2000 km^2 study area (C. Packer personal communication; Packer *et al.* 2005). The project's study area overlaps almost entirely with the survey area, and although the surveys here extend farther east and south, there are very few resident lions in these additional areas (Maddox 2002). We calculated comparable abundance measures from our surveys by multiplying estimated lion density by survey area.

The SCP provided annual estimates of the total number of individual cheetah in an approximately 2200 km^2 study area (Caro 1994; Durant *et al.* 2007). SCP's study area does not entirely overlap with the survey area here; areas beyond the southwest and western boundaries of the survey area are included within the cheetah study area, whereas areas outside the park to the south and east are excluded. Furthermore, unlike the situation with lions, there is likely to be a significant cheetah population in the excluded areas, although there is substantial overlap between both areas. There are two additional sources of discrepancy: (i) the SCP estimate is derived from the number of cheetahs using the area for some or all of the year, whereas the survey estimate is instantaneous; (ii) the SCP estimate is derived from adults, whereas the surveys include cubs. Despite these provisos, the SCP estimates provide an appropriate index from which to compare trends in density. For each survey year, density was calculated by number of adult cheetahs alive at the year end divided by study area and used to provide an index of trend.

POWER ANALYSIS

To explore the ability of distance-based sampling to detect future abrupt population change, we simulated populations fluctuating across a range of coefficient of variations (CV). The population was allowed to fluctuate randomly according to the CV around a constant mean over 2 or 10 surveys (1 wet and 1 dry or 5 wet and 5 dry), then the population dropped to either 80%, 50% or 20% of its former level over 10 000 simulations. For each simulation, we fitted two models of population change assuming an underlying log-normal distribution and: (i) assuming no change in abundance; (ii) assuming a change in the last survey year. We recorded the frequency with which the correct model with a change in abundance was preferred using the AIC.

Results

CARNIVORE SIGHTINGS

A total of 1153 km and 1206 km of transects were driven during the 2002 dry and 2003 wet season survey, respectively, and 1246 km during each season in 2005 (Appendix S1, Supporting Information). Thirteen species of wild and domestic carnivores were sighted, six of which were seen sufficiently frequently for distance-based analysis (> 25 clusters): spotted hyaena, golden jackal, black-backed jackal, bat-eared fox, lion and cheetah. Side-striped jackal (12 sightings) was also included, by modelling its detection function jointly with other jackal species. Species where sightings were insufficient for fitting detection functions were as follows: serval (*Leptailurus serval* Schreber, eight sightings), honey badger (*Mellivora capensis* Schreber, 5), banded mongoose (*Mungos mungo* Gmelin,

3), domestic dog (*Canis lupus familiaris* Linnaeus, 3), wildcat (*Felis silvestris* Schreber, 3) and caracal (*Caracal caracal* Schreber, 2).

PROBABILITY OF DETECTION

The lowest-AIC detection function for spotted hyaenas and cheetahs was half-normal with a cosine adjustment and with species as a covariate; for lions, uniform with one cosine adjustment term; for the canids, a hazard rate with a jackal/fox covariate (Table 1, Fig. 2). All models showed adequate goodness of fit, except for lion where the chi-square value was marginally significant ($P = 0{\cdot}03$) owing to an excess of observations at 50–100 m compared with 100–150. This was not judged sufficiently serious to prevent the use of the model for inference.

For all species, $\hat{p}_i$ was markedly < 1 (Table 1), and hence earlier fixed-width surveys in 1977 and 1986 clearly underestimated numbers, ranging from 84% of lions to only 35% of bat-eared foxes.

Table 1. Detection function model parameters for distance-based surveys analysed by cluster and individual (truncated at 200 m); and fixed-width surveys analysed by individual (truncated at 100 m)

		Analysis by cluster ($w = 200$)							Analysis by individual ($w = 200$)			Old surveys ($w = 100$)	
Species	Model	n_c before	n_c after	χ^2	$\hat{p}_c$	%CV $\hat{p}_c$	$\hat{E}(c)$	%CV $\hat{E}(c)$	n_i after	$\hat{p}_i$	%CV $\hat{p}_i$	$\hat{p}_i$	%CV $\hat{p}_i$
Spotted hyaena	HN– cos(2) with species covariate	494	389	0·32	0·46	3·73	1·91	4·79	742	0·48	2·64	0·71	0·05
Cheetah	HN– cos(2) with species covariate	36	28	0·32	0·43	14·57	1·46	12·9	41	0·46	11·75	0·70	0·05
Lion	Unif + cos(1)	74	58	0·03	0·55	7·53	2·48	15·45	144	0·55	4·74	0·84	0·02
Golden jackal	HR with jackal/fox covariate	178	143	0·31	0·40	5·92	1·57	4·41	224	0·39	4·70	0·58	0·09
Black-backed jackal	HR with jackal/fox covariate	34	30				1·63	6·22	49				0·09
Side-striped jackal	HR with jackal/fox covariate	12	12				1·50	17·41	18				0·09
Bat-eared fox		28	25		0·18	20·90	2·00	7·64	50	0·22	13·40	0·35	0·19

n_c (before and after truncation) and n_i (after truncation) denote number of clusters and individuals, respectively, chi-square goodness of fit of model; $\hat{p}_c$ and $\hat{p}_i$ probabilities of detecting clusters and individuals, respectively (assuming individuals are not clustered), and $\hat{E}(c)$ average cluster size. HN, Unif and HR denote half-normal, uniform and hazard rate key functions; cos(x) denotes a cosine adjustment term of order x.

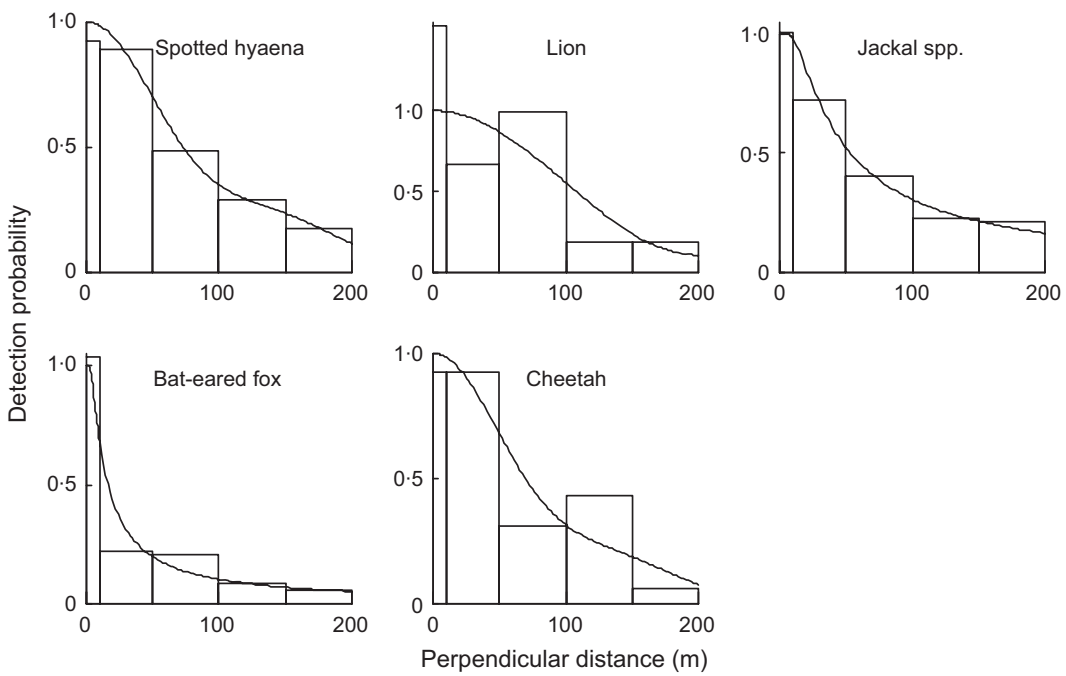

Fig. 2. Observed distances and fitted detection functions.

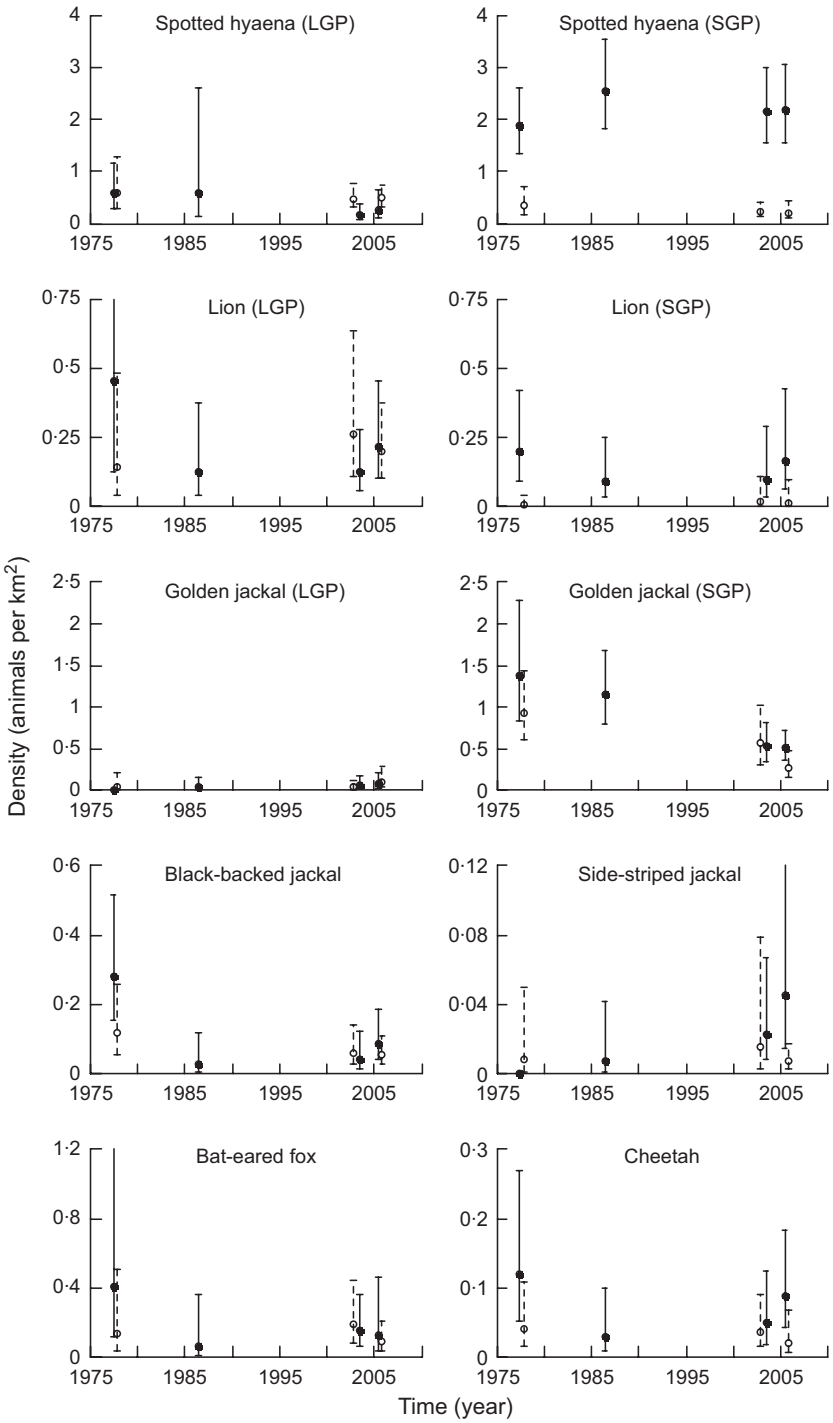

Fig. 3. Density with 95% confidence limits over time. Dashed lines with open circles denote dry season and solid lines with filled circles wet season estimates. More abundant species are split into long (LGP) and short grass plains (SGP) strata.

DENSITY AND POPULATION CHANGE

Spotted hyaena

A total of 494 groups of spotted hyaenas were seen in distance-based surveys with an average group size of 1·9 (Table 1). Many more hyaenas were seen in the wet season than dry season (Fig. 3). The analytical trend analysis suggested that there might be a slow decline in this species at around −0·5% per year; however, this was not confirmed by the more robust bootstrap analysis, nor was there any evidence of abrupt population change (Table 2).

Golden Jackal

Golden jackal were the most frequently seen jackal species, with 178 groups seen in distance-based surveys with average group size 1·6 (Table 1). Densities were much higher on short grass than LGP, but did not vary markedly between seasons (Fig. 3). The species showed a significant long-term decline of

Table 2. Analysis of annual trends and abrupt change using analytical and bootstrap approaches

	Analytic annual trend					Bootstrap annual trend				Abrupt change in last survey			
Species	*r*%	Lower C.L	Upper C.L.	SD	Trend *P*	*r*%	Lower C.L	Upper C.L.	SD	*r*%	Lower C.L	Upper C.L.	SD
Spotted hyaena	**−0·52**	**−0·97**	**−0·05**	**0·24**	**0·03**	−0·50	−1·64	0·72	0·60	−13·40	−40·42	14·12	14·54
Lion	−3·06	−1·57	0·90	0·63	0·57	−0·30	−4·20	4·59	2·25	16·47	−60·32	205·60	72·28
Cheetah	−1·21	−3·24	0·90	1·07	0·25	−1·09	−4·87	3·39	2·10	−25·72	−65·26	47·96	29·16
Golden jackal	**−3·09**	**−3·76**	**−2·43**	**0·36**	**0·00**	**−3·09**	**−4·47**	**−1·71**	**0·70**	**−49·84**	**−60·65**	**−35·48**	**7·23**
Black-backed jackal	**−3·83**	**−5·41**	**−2·23**	**0·86**	**0·00**	**−3·87**	**−6·53**	**−1·19**	**1·35**	−10·70	−55·25	45·20	27·47
Side-striped jackal	6·79	0·86	16·06	3·32	0·06	9·96	−0·38	45·54	13·15	120·86	−87·21	793·39	213·81
Bat-eared fox	**−3·38**	**−5·03**	**−1·69**	**0·89**	**0·00**	**−3·54**	**−6·93**	**−0·09**	**1·74**	−43·61	−89·14	20·63	30·91

r% is percentage annual growth rate and significant trends ($P < 0{\cdot}05$) are in bold.

around 3% per year, amounting to 60% over 28 years (Table 2). The abrupt change analysis suggested a decline of 49% in the last survey, relative to previous surveys (Table 2); however, this result appears to be driven by dry season counts; wet season counts did not reflect this change (Fig. 3).

Black-backed jackal

Black-backed jackal were seen much less frequently than golden jackal; only 34 groups were seen, although average group size was the same (Table 1). There was very little difference in density between seasons. As with golden jackal, black-backed jackal showed a significant long-term decline; nearly 4% per year, totalling nearly 70% between 1977 and 2005. However, there was no evidence of recent abrupt change.

Side-striped jackal

Only 12 groups of side-striped jackal were recorded with average group size 1·5 (Table 1), confirming this species as the least common jackal in the survey area. The analytical trend analysis suggested a possible increase ($P = 0{\cdot}06$) in this species, but this was not confirmed by bootstrap analysis, neither was there evidence of recent abrupt change in population size (Table 2).

Bat-eared fox

Twenty-eight groups of bat-eared foxes were recorded with average group size 2·0 (Table 1). The detection function for this species showed a particularly rapid decline with distance, probably reflecting its smaller size (Fig. 2) and resulted in a high coefficient of variation, averaging 66% in the 2005 wet season, the highest of all species in this study. The species was found in both short and LGP with no difference in density between seasons (Appendix S2, Supporting Information). There was a significant decline in density of 3–4% per year, but no evidence of recent abrupt decline (Table 2).

Lion

A total of 74 groups of lions were recorded, with average group size 2·5 (Table 1). There was no clear difference in lion densities between wet and dry seasons, although densities appeared higher on the SGP and lower on the LGP in the wet than in the dry season (except for 1977) (Fig. 3; Appendix S2, Supporting Information). No significant changes in lion population size were detected over the study (Table 2).

Cheetah

Thirty-six groups of cheetahs were recorded with average group size 1·5 (Table 1). Observations were concentrated on the SGP in the wet season and LGP in the dry season (Appendix S2, Supporting Information), and there was a tendency for more cheetah to be seen in the wet than in the dry season (Fig. 3). No significant changes in cheetah population size were detected (Table 2).

COMPARISON WITH LONG-TERM STUDIES

Lion abundance estimates from transect surveys were reasonably similar to those from SLP's long-term study of individually known lions; however, the estimate from the first survey in 1977 stands out as being overly high (Fig. 4a), suggesting a problem with this survey. Thus, although the SLP estimates show a significant increase from below 200 to over 300 lions, no increase was detected over this study, possibly owing to an inflated estimate in this first survey.

Although it is difficult to directly compare cheetah density estimates from the surveys to SCP's estimates, for reasons outlined earlier, estimates were reasonably similar (Fig. 4b). However, as with lions, the first survey estimate is markedly higher than the SCP estimate. Trends are expected to be directly comparable between the two data sets, and data from SCP show no evidence of significant change in population size, in agreement with our surveys.

POWER ANALYSIS

Average CVs found from distance-based surveys ranged widely from 11% for spotted hyaenas to 66% for bat-eared fox (Appendix S2). The three species seen most often, spotted hyaena, lion and golden jackal, had average CVs mostly between 10 and 35%, whilst the other four species nearly all had CVs of more than 35%. CV had a major impact on power

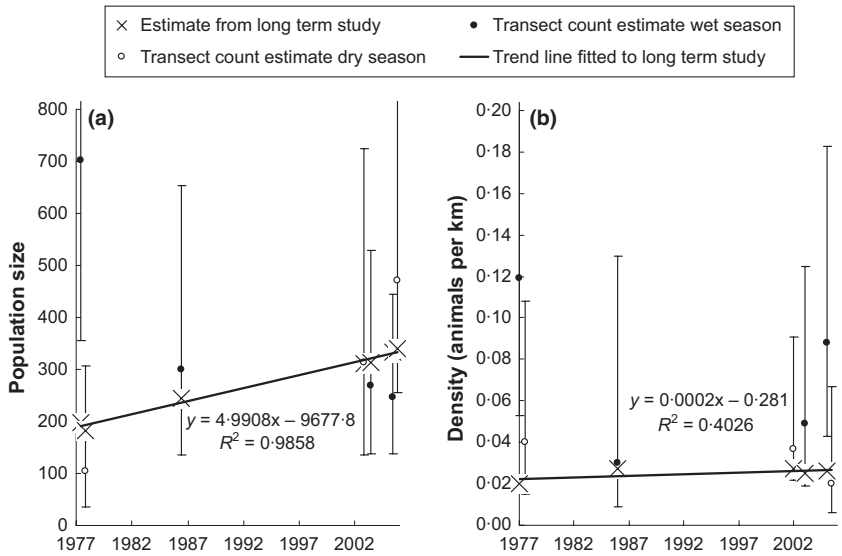

Fig. 4. Estimates from this study compared with (a) abundance estimates for lion and (b) density estimates for cheetah from long-term studies.

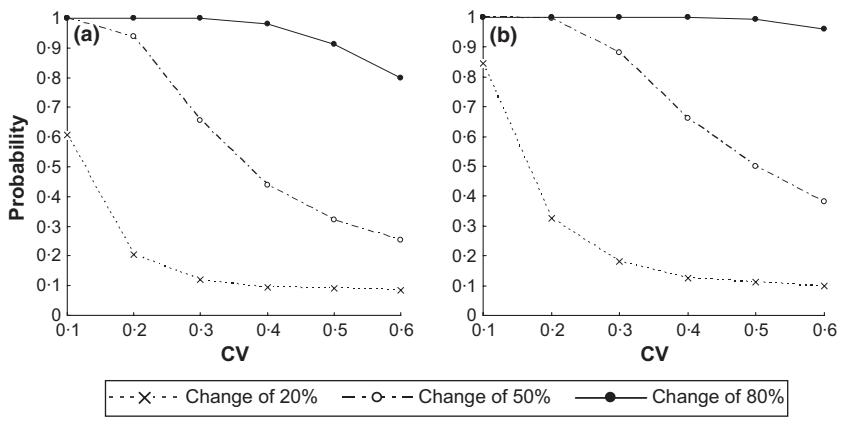

Fig. 5. Power of detecting 20, 50 and 80% change in population size in the last survey year against CV generated by simulation over (a) 2 and (b) 10 year survey cycles.

of detecting population change, and the chance of detecting a percentage abrupt decline of $< 50\%$ decreased markedly with CV (Fig. 5). Detecting a decline of 80% was more robust, particularly over a higher number of surveys. Overall, over 10 surveys, we found that our method should be reasonably good at detecting sudden changes of 20% or more in spotted hyaenas; changes of 50% or more in lions and golden jackal and is likely to detect changes of 50% or more around half the time for the other species. However, the method should be substantially more powerful at detecting long-term trends, as evidenced by our analyses.

Discussion

Our study shows that distance sampling can be used to detect long-term trends and abrupt changes in population size for a significant proportion, seven species in total, of the carnivore community in our study area. Moreover, we were able to use recent information on relationships between detectability and distance to adjust historical data from fixed-width transects, to enable detection of population change over a 28-year period. Of the seven species analysed three, golden and black-backed jackal and bat-eared fox, showed long-term declines in population size, and there was some evidence of abrupt recent decline for one species, golden jackal. Apart for a worryingly inflated count in the first fixed-width survey, estimates appeared to agree with data from two intensive long-term projects on lion and cheetah, supporting the validity of our results, even though lions are nocturnal and counts were made during the day. For smaller nocturnal species, such as bat-eared fox, we might expect our estimates to provide an index of density rather than an absolute estimate. Overall, however, the method is relatively cheap and easy to implement, and thus potentially useful for detecting long-term and abrupt changes in population size, providing important information on carnivore biodiversity which has been historically lacking.

Density variation across seasons and vegetation strata for all species were consistent with results from other studies. Densities of spotted hyaenas were much higher in the wet season than in the dry season, as expected from the commuting system of this species (Hofer & East 1993), whereas both cheetah and lions shifted from long grass onto SGP during the wet season (Schaller 1972; Durant *et al.* 1988). The canids, all of which are territorial (Moehlman 1986), showed no seasonal changes in

densities; however, they selected different habitats. Densities of golden jackals were higher on the short grass than LGP (Fig. 3) as expected for a species found in arid grassland and deserts (Sillero-Zubiri, Hoffmann & Macdonald 2004), whilst black-backed jackals were concentrated on the LGP (Appendix S2, Supporting Information), as expected from its ecology (Sillero-Zubiri, Hoffmann & Macdonald 2004). Lions demonstrated the highest mean group size, reflecting the pronounced sociality found in this species (Packer, Scheel & Pusey 1990).

The four key assumptions of distance sampling were met: (i) Groups of animals are distributed randomly with respect to transects – on the Serengeti plains transects could be systematically assigned without respect to topography; (ii) groups on the transect line are detected with certainty – on open plains there was little possibility of animals being missed if they were on the transect line; (iii) groups are detected at their original location – although some animals moved away as vehicles approached, in the open habitat of the Serengeti it was straightforward for observers to record the distance to where animals were first seen; (iv) measurements are exact – this assumption was not always met; however, the interval estimation method recommended by Buckland *et al*. (2001) was used to help compensate for this, and errors are likely to be small.

Our analysis indicates that the assumption, underlying fixed-width counts in 1977 and 1986, of perfect detectability out to 100 m was unreasonable (Fig. 2) and resulted in an underestimate of density. Our adjustments of these estimates for comparison with distance-based surveys assume that detection has not changed over the 28 years between surveys. There is no reason to suspect that there has been any significant change; although there have been some changes in grass height in the centre of our survey area (Packer *et al*. 2005), these will affect a small proportion of the overall area. Of more significance is likely to be the human tendency to include animals slightly outside fixed-width transects into the survey when technically they should have been excluded (Buckland *et al*. 2001). This might explain the unusually high estimates in first survey in 1977, perhaps because training was less effective. Continued data collection will improve understanding of how detection changes with distance and time and will shed light onto these concerns.

Distance-based transects provided estimates of density of carnivores with greater accuracy (density was underestimated by up to 65% in fixed-width transects) and precision (lower CVs were achieved in distance-based transects) than fixed-width transects. As carnivore encounter rates were low, the extra time involved in estimating distance at each encounter was not excessive. Alternative population estimation methods for carnivores include camera traps, spoor counts and call-ins (Bashir *et al*. 2004), but distance sampling has the advantage that it can be completed within 3 days and is relatively cost-effective if vehicles and manpower are available.

The significant declines observed in golden and black-backed jackals are supported by other evidence. A decline in black-backed jackals in the woodlands was observed in the 1970s and in golden jackals on the SGP in the 1990s (P. Moehlman personal communication). Furthermore, there was a decline in observations of jackals appearing at kills of cheetah between 1980 and 2004 (Hunter, Durant & Caro 2007). The decline in bat-eared foxes is unexpected. There is no immediate explanation for these declines, but disease outbreaks have been recorded in black-backed jackals (Moehlman 1983) and bat-eared foxes (Maas & Macdonald 2004) over the duration of this study. A number of diseases, including canine distemper, parvovirus and rabies, are known to impact carnivore populations (e.g. Mech & Goyal 1995; Packer *et al*. 1999; Randall *et al*. 2006; Lembo *et al*. 2008). Some predator prey systems are characterised by large fluctuations in abundance (e.g. Post *et al*. 2002; Gilg, Hanski & Sittler 2003), but more information is needed to determine whether such dynamics play a role here. Our bootstrap trend analysis found no evidence of change in densities of lion, spotted hyaena, side-striped jackal and cheetah. However, the analytical trend analysis suggested that there may have been declines in spotted hyaena and a possible increase in side-striped jackal and deserves further investigation.

Although the Serengeti plains are unusual in that it is easy to see animals over relatively large distances, our techniques are applicable to other habitats with similar visibility, such as grassland or desert. Moreover, combining rare species with similar sized, but more commonly observed, species aids calculation of the detection function, making the method potentially useful for other habitats where visibility is reduced and detection lower. This study has uncovered some interesting changes in population size within the Serengeti carnivore community; however, further long-term monitoring of these carnivores and the resources on which they depend is needed to fully understand the inter-relationships between these carnivores, their habitat, their prey and human communities bordering the Serengeti. This information will help park managers to make informed decisions about effective management based on a sound understanding of the ecosystem.

Conclusion

The distance methodology provided a more powerful technique for estimating density than fixed-width transects in the Serengeti plains. The surveys provided indices of population density and analysis of population change for seven species of carnivore, allowing monitoring of a substantial subsection of an African carnivore community. Results suggest declines in three species and we recommend focussing further data collection on these species to identify underlying causes. The decline in golden jackal, detected by both the trend analysis and abrupt change analysis, is a particular cause for concern and deserves further investigation. Our results provide the first quantitative evidence of long-term declines, indicating the value of our approach. Without monitoring, it is possible to imagine a species disappearing before conclusive evidence of a decline is detected. Overall, the distance sampling method shows much promise for monitoring carnivore densities and the power analysis provides confidence that large changes of 50% or more can be detected. We therefore recommend further surveys at 1–3 year intervals to tighten

estimates of the detection function, to include more species in density estimates, and provide more power to detect changes in densities. More frequent monitoring would further allow fitting of more complex (and realistic) trend models, such as smooth, nonlinear trends (Thomas, Burnham & Buckland 2004) and would improve power to detect long-term trends (Gibbs 2000). Whilst the Serengeti plains are unusually open and hence are particularly appropriate for this method, our approach indicates that useful data can be obtained from a very low number of sightings of a species provided it can be combined with other species of similar detectability for estimation of the detection function. If carnivores could be combined with more commonly seen species such as warthogs or small antelope, it would open substantial opportunities for wider use of the method.

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References

Balmford, A., Beresford, J., Green, J., Naidoo, R., Walpole, M. & Manica, A. (2009) A global perspective on trends in nature-based tourism. *PLoS Biology*, **7**, e1000144.

Bashir, S., Daly, B., Durant, S.M., Forster, H., Grisham, J., Marker, L., Wilson, K. & Friedmann, Y. (2004) *Global Cheetah (Acinonyx jubatus) Monitoring Workshop Report*. CBSG South Africa, Pretoria.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to Distance Sampling*. Oxford University Press, Oxford.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2004) *Advanced Distance Sampling*. Oxford University Press, Oxford.

Campbell, K.L.I. & Borner, M. (1986) *Census of Predators on the Serengeti Plains May 1986. Serengeti Ecological Monitoring Programme*. TAWIRI, Arusha.

Campbell, K.L.I. & Borner, M. (1995) Population trends and distribution of Serengeti herbivores: implications for management. *Serengeti II: Dynamics, Management and Conservation of an Ecosystem* (eds A.R.E. Sinclair & P. Arcese), pp. 117–145. University of Chicago Press, Chicago.

Caro, T.M. (1994) *Cheetahs of the Serengeti Plains: Group Living in an Asocial Species*. University of Chicago Press, Chicago.

Creel, S. & Creel, N.M. (1996) Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, **10**, 526–538.

Creel, S., Spong, G. & Creel, N. (2001) Interspecific competition and the population biology of extinction-prone carnivores. *Carnivore Conservation*, **5**, 35–60.

Davison, A.C. & Hinkley, D. (2006) *Bootstrap Methods and their Application*, 8th edn. Cambridge University Press, Cambridge.

Durant, S.M. (1998) Competition refuges and coexistence: an example from Serengeti carnivores. *Journal of Animal Ecology*, **67**, 370–386.

Durant, S.M. (2000a) Living with the enemy: avoidance of hyaenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, **11**, 624–632.

Durant, S.M. (2000b) Predator avoidance, breeding experience and reproductive success in endangered cheetahs (*Acinonyx jubatus*). *Animal Behaviour*, **60**, 121–130.

Durant, S.M., Caro, T.M., Collins, D.A., Alawi, R.M. & FitzGibbon, C.D. (1988) Migration patterns of Thomson's gazelles and cheetahs on the Serengeti plains. *African Journal of Ecology*, **26**, 257–268.

Durant, S.M., Bashir, S., Maddox, T. & Laurenson, M.K. (2007) Relating long-term studies to conservation practice: the case of the Serengeti Cheetah Project. *Conservation Biology*, **21**, 602–611.

Fewster, R.M. (2011) Variance Estimation for Systematic Designs in Spatial Surveys. *Biometrics*, **67**. doi: 10.1111/j.1541-0420.2011.01604.x.

Fewster, R.M., Buckland, S.T., Burnham, K.P., Borchers, D.L., Jupp, P.E., Laake, J.L. & Thomas, L. (2009) Estimating the encounter rate variance in distance sampling. *Biometrics*, **65**, 225–236.

Gerrodette, T. (1987) A power analysis for detecting trends. *Ecology*, **68**, 1364–1372.

Gibbs, J.P. (2000) Monitoring Populations. *Research Techniques in Animal Ecology: Controversies and Consequences* (eds L. Boitani & T. Fuller), pp. 213–252. Columbia University Press, New York.

Gilg, O., Hanski, I. & Sittler, B. (2003) Cyclic dynamics in a simple vertebrate predator-prey community. *Science*, **302**, 866–868.

Ginsberg, J.R. (2001) .L. Setting priorities for carnivore conservation: what makes carnivores different? *Carnivore Conserva* (eds J.L. Gittleman, S.M. Funk, D.W. MacDonald & R.K. Wayne), pp. 498–523. Cambridge University Press, Cambridge.

Grogger, J.T. & Carson, R.T. (1991) Models for truncated counts. *Journal of Applied Econometrics*, **6**, 225–238.

Hedley, S.L., Buckland, S.T. & Borchers, D.L. (2004) Spatial distance sampling models. *Advanced Distance Sampling: Estimating Abundance of Biological Populations* (eds S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers & L. Thomas), pp. 48–70. Oxford University Press, Oxford.

Hofer, H. & East, M.L. (1993) The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. II. Intrusion pressure and commuter's space use. *Animal Behaviour*, **46**, 547–557.

Hofer, H. & East, M.L. (1995) Population dynamics, population size, and the commuting system of Serengeti spotted hyaenas. *Serengeti II: Dynamics, Management and Conservation of an Ecosystem* (eds A.R.E. Sinclair & P. Arcese), pp. 332–363. University of Chicago Press, Chicago.

Hunter, J.S., Durant, S.M. & Caro, T.M. (2007) Patterns of scavenger arrival at cheetah kills in Serengeti National Park Tanzania. *African Journal of Ecology*, **45**, 275–281.

Kamler, J.F., Ballard, W.B., Gilliland, R.L., Lemons, P.R. & Mote, K. (2003) Impacts of coyotes on swift foxes in northwestern Texas. *Journal of Wildlife Management*, **67**, 317–323.

Kruuk, H. (1972) *The Spotted Hyena: A Study of Predation and Social Behavior*. University of Chicago Press, Chicago.

Laurenson, M.K. (1994) High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care. *Journal of Zoology*, London, **234**, 387–408.

Lembo, T., Hampson, K., Haydon, D.T., Craft, M., Dobson, A., Dushoff, J., Ernest, E., Hoare, R., Kaare, M. & Mlengeya, T., Mentzel, C. and Cleaveland, S. (2008) Exploring reservoir dynamics: a case study of rabies in the Serengeti ecosystem. *Journal of Applied Ecology*, **45**, 1246–1257.

Maas, B. & Macdonald, D.W. (2004) Bat-eared foxes. *Biology and Conservation of Wild Canids* (eds D.W. Macdonald & C. Sillero-Zuberi), pp. 227–242. Oxford University Press, Oxford.

Maddox, T. (2002) The ecology of cheetahs and other large carnivores in a pastoralist-dominated buffer zone. PhD Dissertation, University of London.

Mech, L.D. & Goyal, S.M. (1995) Effects of canine parvovirus on gray wolves in Minnesota. *Journal of Wildlife Management*, **59**, 565–570.

Moehlman, P.D. (1983) Socioecology of silver-backed and golden jackals, *Canis mesomelas* and *C. aureus*. *Recent Advances in the Study of Mammalian Behavior* (eds J.F. Eisenberg & D.G. Kleiman), pp. 423–438. American Society of Mammalogists, Lawrence, Kansas.

Moehlman, P.D. (1986) Ecology of cooperation in canids. *Ecological Aspects of Social Evolution* (eds D.I. Rubenstein & R.W. Wrangham), pp. 64–86. Princeton University Press, Princeton.

Okello, M.M., Manka, S.G. & D'Amour, D.E. (2008) The relative importance of large mammal species for tourism in Amboseli National Park, Kenya. *Tourism Management*, **29**, 751–760.

Packer, C., Scheel, D. & Pusey, A.E. (1990) Why lions form groups: food is not enough. *American Naturalist*, **136**, 1–19.

Packer, C., Altizer, S., Appel, M., Brown, E., Martenson, J., O'Brien, S.J., Roelke-Parker, M., Hofmann-Lehmann, R. & Lutz, H. (1999) Viruses of the Serengeti: patterns of infection and mortality in African lions. *Journal of Animal Ecology*, **68**, 1161–1178.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S. & Sinclair, A.R.E. (2005) Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science*, **307**, 390–393.

Palomares, E. & Caro, T.M. (1999) Interspecific killing among mammalian carnivores. *American Naturalist*, **153**, 492–508.
Post, E., Stenseth, N.C., Peterson, R.O., Vucetich, J.A. & Ellis, A.M. (2002) Phase dependence and population cycles in a large-mammal predator-prey system. *Ecology*, **83**, 2997–3002.
Randall, D.A., Marino, J., Haydon, D.T., Sillero-Zubiri, C., Knobel, D.L., Tallents, L.A., Macdonald, D.W. & Laurenson, M.K. (2006) An integrated disease management strategy for the control of rabies in Ethiopian wolves. *Infectious Disease and Mammalian Conservation*, **131**, 151–162.
Schaller, G.B. (1972) *The Serengeti Lion: A study of predator-prey relations*. University of Chicago Press, Chicago.
Sechrest, W., Brooks, T.M., da Fonseca, G.A.B., Konstant, W.R., Mittermeier, R.A., Purvis, A., Rylands, A.B. & Gittleman, J.L. (2002) Hotspots and the conservation of evolutionary history. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 2067–2071.
Serengeti Research Institute (1977a) Census of predators and other animals on the Serengeti plains, May 1977. Serengeti National Park.
Serengeti Research Institute (1977b) Census of predators and other animals on the Serengeti plains, October 1977. Serengeti National Park.
Sillero-Zubiri, C., Hoffmann, M. & Macdonald, D.W. (2004) *Canids: Foxes, Wolves, Jackals and Dogs, Status Survey and Conservation Action Plan*. IUCN/SSC Canid Specialist Group, Gland, Switzerland and Cambridge, UK.
Sinclair, A.R.E. & Arcese, P. (1995) *Serengeti II: Dynamics, Management and Conservation of an Ecosystem*. University of Chicago Press, Chicago.
Thomas, L., Burnham, K.P. & Buckland, S.T. (2004) Temporal inferences from distance sampling surveys. *Advanced Distance Sampling* (eds S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers & L. Thomas), pp. 71–107. Oxford University Press, Oxford.
Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A. & Burnham, K.P. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, **47**, 5–14.
Wayne, R.K., Van Valkenburgh, B., Kat, P.W., Fuller, T.K., Johnson, W.E. & O'Brien, S.J. (1989) Genetic and morphological divergence among sympatric canids. *Journal of Heredity*, **80**, 447–454.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Realized survey effort (LGP denotes long grass plains and SGP short grass plains).

Appendix S2. Carnivore density and abundance per season, year, and habitat (D is density, N is abundance, CI confidence interval).

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