Estimating carnivore densities for conservation purposes: indirect methods compared to baseline demographic data

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Using the cheetah *Acinonyx jubatus* as a model, we compared predictions from four indirect methods of estimating carnivore densities to estimates of density derived from baseline demographic data collected during behavioural ecological studies in three national parks of East Africa. Interviewing people locally was the most accurate indirect method and produced estimates representing 75 to 100% of reference densities. Regressing cheetah biomass against prey biomass further underestimated reference densities. Using an average cheetah density derived from reported densities in 13 African protected areas, and modeling cheetah densities from home range and demographic data were the least accurate approaches. When indirect methods' results were compared across ten study areas in East Africa, we found that log-transformed interview and prey biomass methods' estimates were significantly correlated, and that prey biomass and home range models produced significantly different outcomes. After discussing strengths and weaknesses of the methods, we outline the conditions under which each may provide valid results. Our findings highlight the importance of calibrating indirect methods of estimating carnivore densities, and demonstrate the difficulties that conservation planners face in integrating density estimates derived from different methods when devising conservation strategies.

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Large carnivores hold a prominent position in conservation biology for at least four reasons. First, large carnivores are sensitive indicators of ecosystem integrity since they survive only where lower trophic levels remain relatively undisturbed (Kucera and Zielinski 1995). Second, because large carnivores are wide ranging, their effective conservation insures that substantial areas of wilderness are preserved (Foreman 1993). Third, presently large carnivores typically live in small isolated populations and are therefore particularly prone to extinction through stochastic events and habitat disruption (Meffe and Carroll 1994). Finally, many large carnivore populations suffer directly from human interference through over-exploitation by trophy hunting (Owens and Owens 1985), trade in body parts (Jackson and Kempf 1994), or through defence of domestic livestock (Novaro 1995).

Effective conservation strategies hinge on reliable knowledge of population sizes, but estimating the size of carnivore populations is made particularly difficult by their secretive nature, often nocturnal habits, and low densities. Nevertheless, carnivore densities can be directly estimated by identifying all individuals within a population. Individuals are generally recognised using their natural markings (e.g. lions, *Panthera leo*, Bertram 1978; wild dogs, *Lycaon pictus*, Frame et al. 1979; cheetahs, *Acinonyx jubatus*, Caro and Durant 1991). Unfortunately, identifying individual carnivores within a population requires years of intensive field work, and this approach is limited to populations in relatively

open habitats. Therefore, a number of alternative methods have been devised to estimate carnivore densities (Bertram 1976). These methods fall into five categories, each with specific advantages and limitations.

The first category regroups methods using ground and aerial transects to count carnivores (e.g. spotted hyaenas, *Crocuta crocuta* Hofer and East 1995, and wolves, *Canis lupus*, Fuller 1982). These methods largely underestimate densities because carnivores are well camouflaged (Kruuk 1972; but see Fuller 1982).

The second category of methods may be termed 'mark-resighting'. Carnivores are typically trapped or immobilized, marked, and then released (e.g. black bears, *Ursus americanus*, Lindzey 1982; tigers, *Panthera tigris*, Karanth 1995). Population size is estimated from the ratio of marked to unmarked individuals in the population using the Lincoln index (Caughley 1977). Although quicker than identifying each individual within a population, these methods are still time consuming and often invasive. Furthermore, density estimates are often inaccurate since two of the assumptions of the model (equal catchability and random mixing of marked individuals in the population) are generally violated (Caughley 1977).

The third category of methods derives estimates of carnivore densities (henceforth referred to as carnivore densities) from signs of carnivores' presence in the field. Signs include active dens (e.g. European badger, *Meles meles*, Harris et al. 1992; red foxes, *Vulpes vulpes*, Phillips 1982), tracks (e.g. tigers, Panwar 1979; cougars, *Felis concolor*, Smallwood and Fitzhugh 1995; coyotes, *Canis latrans*, Linhart and Knowlton 1975), and combinations of scats and tracks (e.g. Iberian lynx, *Felis pardina*, Palomares et al. 1991). The advantage of these approaches is that individuals do not need to be observed directly, and results can therefore be obtained relatively quickly. Unfortunately, the relationship between sign density and population size is rarely known (Caughley 1977). Nevertheless, these methods are good at estimating trends in population sizes over time.

A fourth set of methods involves public participation. People are interviewed about their sightings of carnivores (e.g. wild dogs, Fanshawe et al. 1991) or are asked to provide photographs (wild dogs, Maddock and Mills 1993). These methods are relatively quick and inexpensive and can be conducted over a large spatial scale, but results can suffer from unreliable reporting and incomplete coverage.

The last series of methods attempts to model predator densities based on habitat quality, including prey biomass (e.g. tigers, Smith et al. 1987; wolves, Mladenoff et al. 1995). Provided that adequate background data are available, these methods require relatively little time and money. The accuracy of the results depends on identifying the pertinent habitat variables influencing the abundance of a given carnivore, on weighting them correctly in the model, and on entering accurate measurements of these variables.

Although these diverse methods are widely used to estimate density of carnivores, there have been remarkably few attempts to calibrate their results to actual numbers of predators in the field (but see Karanth 1987, Borner 1992). As a result there is little basis on which to compare densities using the same method in locations that differ ecologically. Lack of calibration can also affect estimation of population trends at a given location if ecological conditions vary over time. In addition, to our knowledge estimates obtained for a given carnivore population by different indirect methods have never been compared, although conservation biologists and managers usually rely on these various indirect methods to assess predator densities at regional or national levels (Rabinowitz 1993).

In this paper we calibrate four indirect methods of estimating carnivore densities over large spatial scales against population sizes of individually recognized animals derived from demographic data collected in the course of three studies of behavioural ecology. We then compare these indirect methods across a wider sample of areas in order to assess the extent of agreement between them. Our indirect methods are derived from information on the ecology, demography, and behaviour of the cheetah, a species that has been studied in enough African settings to provide data for such comparisons.

Methods

Indirect method 1 – Interviews

This method estimates cheetah densities from sighting reports of cheetahs collected through interviews. P.M.G. conducted interviews in 10 study areas in Kenya (in July and September 1990) and Tanzania (between September 1993 and May 1994): Amboseli, Meru, Nairobi, Serengeti, and Tarangire National Parks; Lake Bogoria, Masai Mara and Samburu National Reserves; Taita Hills Game Sanctuary; and a cattle ranching region in Laikipia District, Kenya. Biologists, park staff, and tourists in protected areas, and farmers in Laikipia District, were asked to report their sightings of cheetahs specifying the date and exact location of each observation, as well as the number, age class, and, when possible, sex of the cheetahs observed (Gros unpubl.). Serengeti National Park was the only study area where cheetah research was taking place while interviews were conducted. There, scientists were not asked for specific cheetah sightings to avoid creating a spurious relationship between interview and field data.

Because some adult male cheetahs live in long-lasting associations of two to five individuals, and because females and their cubs remain together as family groups of up to seven members for an average of 18 months (Caro 1994), it was possible to recognize different

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groups within the bulk of cheetah sightings in each study area. Nonetheless, we could not know the actual number of groups of any reported size and composition, nor the total number of single adults of each sex. To stay on the conservative side, all similarly composed cheetah sightings were considered to describe the same animals, unless sightings were made simultaneously in two separate locations. After discarding potentially redundant sightings, cheetah density was computed by adding up all cheetahs in the remaining sighting reports, and dividing by the area of the reserve or ranching region.

Three types of error are likely to affect cheetah densities obtained by the interview method. First, error in aging or sexing cheetahs, observation of individuals temporarily separated from their group, or simply poor memory can yield incorrect reports. Second, the assumption that all reports of groups of similar size and composition describe a single group of cheetahs may lead to underestimate the actual number of individuals. Third, cheetah population size may be underestimated in areas that are little visited and in those with closed vegetative cover.

Indirect method 2 – Average density

Averaging cheetah densities reported for 13 protected areas in Eastern and Southern Africa (Table 1), we

obtained a density of 0.021 cheetah/km^2. We estimated cheetah population sizes in our ten study areas (listed under method 1) by multiplying this average density parameter by the size of each area.

Three major sources of error can affect cheetah densities obtained by this method. The densities averaged were informed guesses which are generally considered less valid than estimates based on field measurements (but see Caughley 1977). These informed guesses were derived by different scientists. The areas for which densities were available varied considerably in size and ecological attributes.

Indirect method 3 – Prey biomass

East (1984) showed that the biomass of large African savanna predators was significantly correlated with the biomass of their preferred size class of prey. Cheetahs prefer herbivores weighing 15 to 60 kg. We adopted East's approach, using some of his original data and additional pairs of prey–cheetah biomass (Table 1). Unit weights for prey species were obtained from Coe et al. (1976) and cheetah weight from Schaller (1972). The existence of a strong correlation between cheetahs and 15 to 60 kg prey biomass was confirmed (Fig. 1), and we used the associated regression equation ($y = 0.002x + 0.21$, $r^2 = 0.616$, $p = 0.0071$, $n = 10$) to predict

Table 1. Data used to derive prey biomass and cheetah densities. An author's name followed by a date in brackets, e.g. Mills (1990), indicates personal communication. Where several sources are reported, a mean of all available figures was taken to compute cheetah or prey biomass.

| Area	Prey biomass in kg/km^2	Origin of data	Cheetah density in cheetah per km^2	Origin of data
Amboseli National Park	194	Western 1975; East 1988	na	na
Chobe National Park (CNP)	117	CNP counts for 1988	0.002	Wittman (1988)
Etosha National Park	16	East 1989; Stander 1991	0.002	Wittman (1988); Stander 1991
Gonarhezou National Park	na	na	0.006	Myers 1975; Wilson 1987
Hwange National Park	30	East 1984; East 1989	0.006	Wilson 1975; Myers 1975
Itala Game Reserve	618	Wittman (1988)	0.048	Wittman (1988)
Kalahari Gemsbok National Park	24	East 1984; East 1989; KGNP counts for 1987–88	0.005	Mills (1988); Knight (1988)
Kruger National Park	246	East 1984; East 1989; KNP counts for 1982–87–88	0.012	Pienaar 1969; Mills (1990)
Laikipia ranches	72	Mbugua, 1986; East 1988	na	na
Masai Mara National Reserve	410	Broten and Said, 1995	na	na
Mkomazi Game Reserve	25	East 1988; MGR counts 1988	0.011	East 1984
Mkuzi Game Reserve	1254	Wittman (1988); East 1989	0.04	Wittman (1988)
Nairobi National Park	461	McLaughlin 1970; East 1984; East 1988	na	na
Ngorongoro Conservation Area	490	Laurenson 1995	0.012	Laurenson 1995
Samburu National Reserve	183	East 1988	na	na
Serengeti National Park	468	Laurenson 1995	na	na
Narok District	na	na	0.021	Graham and Parker 1965
Tarangire National Park	130	East 1988	na	na
Timbavati Natural Reserve	na	na	0.05	Myers 1975
Umfolozi-Hluhluwe Game Reserve	700	East 1984; Wittman (1988)	0.059	East 1984; Wittman (1988)
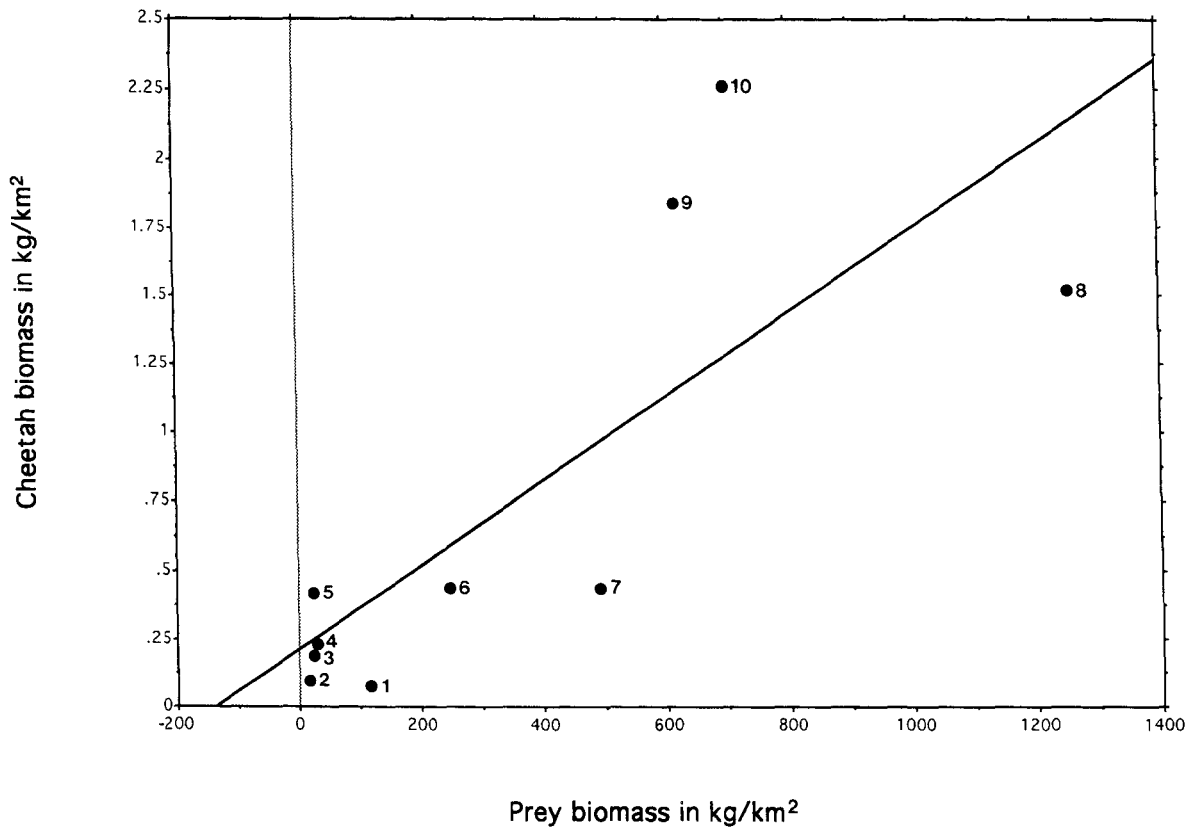
Fig. 1. Relationship between cheetah biomass and biomass of herbivores in the 15–60 kg range ($y = 0.002x + 0.21$, $r^2 = 0.616$, $p = 0.0071$, $n = 10$). 1. Chobe National Park; 2. Etosha National Park; 3. Kalahari Gemsbock National Park; 4. Hwange National Park; 5. Mkomazi Game Reserve; 6. Kruger National Park; 7. Ngorongoro Conservation Area; 8. Mkuzi Game Reserve; 9. Itala Game Reserve; 10. Umfolozi-Hluhluwe Game Reserve.

cheetah densities in the study areas for which prey densities were available (Table 1).

Weaknesses of this method are that the cheetah densities used to compute the regression were derived from informed guesses often made at a different time from when prey densities were measured; the model includes only prey species with unit weights of 15 to 60 kg, but young of larger herbivores also fall prey to cheetahs before they reach 60 kg; moreover cheetahs sometimes consume smaller prey such as hares (Caro 1994). Finally population estimates were not always available for each potential prey species weighing 15 to 60 kg.

Indirect method 4 – Home range

In theory, the number of cheetahs using an area is restricted by the ranging patterns of individuals and the extent to which they can exploit resources simultaneously (Begon et al. 1990). The rationale of the home range method is to derive the maximum number of adult female cheetahs that can share a given amount of

space based on the average female home range size and degree of home range overlap, and then to extrapolate total population size from the number of adult females using a demographic equation. We calculated average female home range size and degree of overlap between female home ranges in the Serengeti Plains. We based our model on female home ranges because females are more philopatric than males (Caro 1994), and because most females follow a similar migratory pattern across the plains (Durant et al. 1988) while males can either be territorial and restricted in space, or floaters covering large areas (Caro and Collins 1986).

Using the Arc Info Geographic Information System, M.J.K. mapped the sighting locations of all known adult females ($N = 51$) on the Serengeti Plains in 1988, a year for which a particularly large data set was available. Female home ranges were drawn applying the minimum convex polygon method (Mohr 1947) (Fig. 2). We then overlaid a 1 by 1 km grid over the map of the study area, picked 30 grid squares at random, counted how many female home ranges overlapped in each of these 30 squares, and took an average of these figures. We limited our sample to 30 squares

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after establishing that the number of overlapping female home ranges stabilized after that many squares were picked.

On the central Serengeti Plains (1738 km²) annual average female home range size was 414 km², based on home range size of all radio-collared females located more than 10 times during 1988 ($N = 11$). An average of 4.82 female home ranges overlapped at any given point of the study area.

Total population size was derived from the number of adult females using the following equation:

$$P = F\{1 + Sr + [(Fc/F) \times Cb] + [(Sad//F) \times Ss]\}$$

where P = population size; F = number of adult females; Sr = adult sex ratio = number of adult females/ number of adult males; Fc = number of adult females accompanied by cubs; Cb = average number of cubs accompanying their mother, regardless of cub age; Sad = number of subadult groups, including singletons; Ss = average size of subadult group. Establishing the value of each equation parameter based on the proportions of the different age and sex classes in the 1988 Serengeti cheetah population we obtained:

$$P = F \times [1 + 0.66 + (0.474 \times 2.43) + (0.39 \times 1.98)]$$

$$= F \times 3.54$$

This equation gives a population of 72 cheetahs for the Serengeti Plains, i.e. 62% of the 116 individually recognised animals observed within the park during 1988. This discrepancy does not necessarily indicate a bad fit of the model: our equation attempted to predict the number of resident cheetahs, while some of the observed cheetahs were seen unfrequently and could have been temporary visitors to the Plains. To estimate cheetah density in each of our study areas, we first estimated the number of adult females by dividing the size of the study area by the average female home range size (414 km²) and then multiplying the result by the average female home range overlap (4.82). We finally multiplied the estimated number of females by the demographic factor of the equation (3.54).

The model's predictions might be inaccurate for several reasons. The demographic factor might have been inflated by including some transient cheetahs when computing ratios of different sex and age classes. Moreover, the extent of home range overlap was likely

LEGEND

▨ Woodlands

▢ Plains

Female Cheetahs

▨ Dutwa

▨ Sarah

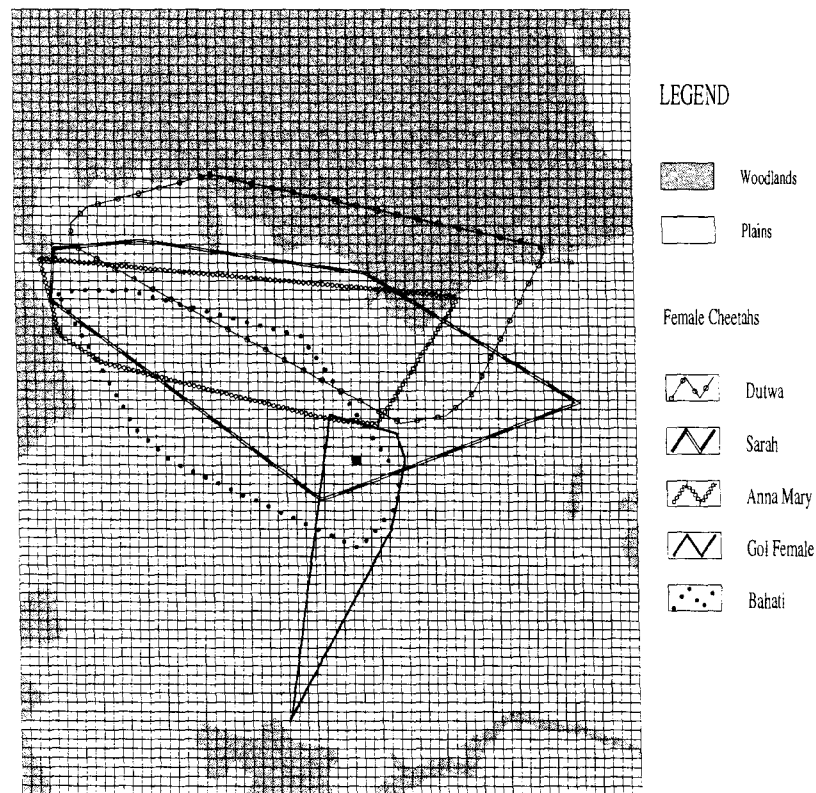▨ Anna Mary

▨ Gol Female

▨ Bahati

Fig. 2. Spatial distribution of female cheetah home ranges on the Serengeti Plains in 1988. For clarity only home ranges of five out of the 51 known females are mapped. A 1 by 1 km grid was used to calculate female territories size and overlap. For example, three territories overlap at the black square.

underestimated since many females were observed less than ten times in 1988. The average home range size could be inaccurate since there was a lot of variation in sizes of radio-collared females' home ranges. Finally, when predicting cheetah densities in our nine study areas, we had to assume that cheetah demography and ranging patterns in these areas were similar to those in Serengeti, but one can expect that local ecological conditions will affect life history parameters and spatial distribution of individuals (Messier 1985, Sandell 1989).

Direct method – Baseline demographic data

Long term studies of the behavioural ecology of cheetahs based on recognition of individual animals have been conducted in only three protected areas: Nairobi National Park (McLaughlin 1970, Eaton 1974) over 22 months, Masai Mara National Reserve (Burney 1980) over 17 months, and Serengeti National Park (Frame and Frame 1981, Caro 1994) over 20 years. In each study, researchers built up an identification file of different animals by recording spot and tail banding patterns, and hence derived a total population size. They also collected detailed information on the age and sex classes and reproductive parameters of cheetahs within these populations. We used densities from the three field studies as a reference with which to assess the validity of the four indirect methods discussed in this paper. While computing cheetah density in the Masai Mara Game Reserve from his field data, Burney (1980) took into account the proportion of sightings of known individuals inside and outside of the reserve. To be consistent with reference densities in Nairobi and Serengeti National Park, we recalculated cheetah density in Masai Mara by adding up all known cheetahs that used the reserve during Burney's study regardless of the time they spent in it, and obtained a density of 0.028 cheetah/km².

Although individual recognition of cheetahs appears to be the most powerful method of estimating population size, it may still underestimate real numbers for two main reasons. First, the derived population size is influenced by the amount of time spent in the field. Even after five years, new adult males were being found by Caro and Collins (1986) in the Serengeti National Park. Therefore, for relatively short field studies, one can expect more accurate results for small protected areas, such as Nairobi National Park, where most individuals are likely to be found quickly. Second, the method relies on obtaining fairly clear photographs or making drawings of individuals, and for this cheetahs need to be relatively tolerant of the observer's vehicle. In most populations there will be an unknown number of shy individuals that elude documentation.

Finally, the four indirect methods of estimating cheetah densities and the baseline demographic data relied on parameters measured at different times between 1970 and 1994. When using the baseline demographic data as our reference for comparing the validity of indirect methods, we assumed that cheetah population sizes in protected settings changed little over time. We also assumed this when measuring agreement between indirect methods. Unfortunately no data are available on the amplitude of variation in cheetah numbers within protected areas over time.

Results

Accuracy of indirect methods

In relation to reference demographic data, the interview method was the most accurate of the four indirect methods. Table 2 presents the accuracy of each indirect-method's prediction, expressed as a percentage of reference density, for three protected areas. For each method,

Table 2. Accuracy of four indirect methods of assessing cheetah density expressed as a percentage of densities from long term studies of cheetah behavioural ecology.

Protected area	Method	Cheetah density (individuals/km²)	Method accuracy (% of reference density)
Masai Mara National Reserve	Reference. Burney, 1980	0.028	na
	Method 1. Interviews	0.021	75
	Method 2. Average density	0.021	75
	Method 3. Prey biomass	0.027	96
	Method 4. Home range	0.041	146
Nairobi National Park	Reference. McLaughlin, 1970	0.094	na
	Method 1. Interviews	0.094	100
	Method 2. Average density	0.021	22
	Method 3. Prey biomass	0.031	32
	Method 4. Home range	0.041	44
Serengeti National Park	Reference. S. Durant, pers. comm.	0.049	na
	Method 1. Interviews	0.044	90
	Method 2. Average density	0.021	43
	Method 3. Prey biomass	0.031	61
	Method 4. Home range	na	na

Table 3. Cheetah densities predicted by the four indirect methods in study areas. NP stands for National Park, NR for National Reserve, and GS for Game Sanctuary.

Area	Interview	Average density	Prey biomass	Home range
Amboseli NP	0.0153	0.021	0.0128	0.0412
Laikipia ranches	0.0109	0.021	0.0081	0.0412
Serengeti NP	0.0438	0.021	0.0302	0.0412
Nairobi NP	0.0941	0.021	0.0297	0.0412
Masai Mara NR	0.0211	0.021	0.0271	0.0412
Samburu NP	0.0218	0.021	0.0124	0.0412
Tarangire NP	0.0091	0.021	0.0104	0.0412
Lake Bogoria NR	0.0187	0.021	na	0.0412
Meru NP	0.0138	0.021	na	0.0412
Taita hills GS	0.0619	0.021	na	0.0412

we substracted each of the three accuracy figures from 100% and divided by three to obtain an average deviation from reference density. This was 12% for the interview method, 37% for the prey biomass method, 51% for the home range method, and 53% for the average density method. The number of reference areas was too low to test for the statistical significance of this result. While interview, prey biomass, and average density methods consistently underestimated prey density, the home range model showed no consistent bias.

Agreement between indirect methods

We ran a multiple comparison using the Wilcoxon matched pairs signed rank test to measure agreement between the four indirect methods' predictions (Table 3). We set the experimentwise error rate at 0.1 to minimize the probability of making a type II error. Each individual test was adjusted to a significance level of $1 - (1 - 0.1)^{1/5} = 0.02$ (Sokal and Rohlf 1981). Prey biomass estimates were significantly greater than home range estimates $(Z = -2.366; p = 0.018)$. None of the other methods produced significantly different estimates: interview vs average density, $Z = -0.255, p = 0.799$; prey biomass vs average density, $Z = -0.676, p = 0.499$; interview vs home range, $Z = -1.274, p = 0.203$; interview vs prey biomass, $Z = -1.521, p = 0.128$.

We further investigated the relationship between interview and prey biomass methods, the two methods which did not produce fixed densities. Data transformed using a logarithmic transformation achieved normality, and we found a linear relationship between the log-transformed density estimates: log (prey biomass density) = 0.568 log (interview density) − 0.848, $r^2 = 0.702; p = 0.0185$.

Discussion

Accuracy of indirect methods

Taking baseline demographic data as a reference, the interview method provided the most accurate results.

This can be partially explained by the fact that both methods rely on a similar approach: recording observations of cheetahs and attempting to identify individuals observed. Results from Nairobi National Park (100% of reference density) show that interviews can produce very accurate estimates in small and highly visited protected areas. The Serengeti National Park estimate was, however, remarkably high (90%) considering that information was gathered for an area of nearly 2000 km². Seasonal concentrations of cheetahs within their migratory range (Durant et al. 1988) may provide the opportunity to observe most of the Plains' population in a more restricted space. The prediction for Masai Mara National Reserve was not as accurate (75%) as for the other two parks, possibly because cheetahs are harder to spot in the relatively closed vegetation of the reserve than in more open landscapes of the Serengeti Plains and Nairobi National Park.

Prey biomass predictions consistently underestimated reference cheetah densities. One reason could be that small and medium sized herbivore densities are often underestimated by aerial censuses (Norton-Griffiths 1978); and another reason could be that young of the abundant migratory herbivores larger than 60 kg, which are not included in the model, also fall prey to cheetahs.

Predictions from the home range model, underestimated (44%) the total cheetah population size in Nairobi National Park. Although the predicted number of female cheetahs was lower than in the reference study, most of the error was due to the demographic part of the model. This is likely because cheetahs have unusually large litter sizes and subadult group sizes in Nairobi National Park (McLaughlin 1970, Gros unpubl.). The model overestimated cheetah density in Masai Mara National Reserve for reasons that are not yet clearly understood.

The average density method largely underestimated reference densities in Nairobi and Serengeti National Parks, likely because cheetah densities are high in these two parks compared to most other sites in Africa (average cheetah density for 18 protected areas including Serengeti and Nairobi: 0.032/km²; average of Serengeti and Nairobi densities alone: 0.071/km²) (see

Table 1 and Gros unpubl.). Cheetah density in Masai Mara stands closer to the average density parameter (0.021 cheetah/km^2) and was therefore better predicted by the model.

Agreement between indirect methods

Our main finding was that densities derived from interviews correlated with those from the prey biomass method, after transformation. This finding is interesting because the two methods estimate cheetah density in independent ways. Concordance between predictions by two indirect methods could simply reflect a similar type of bias, yet comparison to known cheetah reference densities showed that the interview method was relatively accurate. This suggests that both methods produce useful predictions. Interview and prey biomass methods can be used concomitantly when monitoring cheetah densities since the exact relationship between their estimates is known.

Prey biomass and home range models produced significantly different results; probably because each model relies on several estimates (i.e. prey densities; home range size and overlap and demographic parameters respectively), which opens up the potential for error. Using data obtained by these different models to monitor changes in carnivore abundance is therefore not advisable.

Recommendations

Conservation planning often requires rapid assessment of carnivore population sizes to formulate policy, and consequently, indirect methods of estimating densities are frequently used. Our results suggest that each indirect method may be best employed only under a certain set of circumstances.

The interview method provides accurate cheetah density estimates in highly visited areas. It offers an inexpensive option for efficiently assessing cheetah density in small protected areas where it could be carried out by reserve staff. The prey density method gives a good first approximation of cheetah density if local cheetah prey preferences are known and if a reliable prey census is available. The average density method can be expected to produce good estimates of cheetah densities only when used across areas with comparable ecological conditions and human pressures. Extrapolating densities derived from detailed studies in cheetah strongholds leads to overestimating densities in less suitable cheetah habitats. The home range method reflects the idiosyncrasy of cheetah demography and spatial organization in the area used to build the model (home range size, for example, is very 'park-specific'). Therefore the home range method should be best used

to back up interview or average density predictions rather than as a unique density estimator. Since, we found no consistency between home range and prey biomass densities, these two methods should not be used in conjunction with each other.

We used the cheetah to investigate indirect methods of assessing carnivore densities because data needed to apply these methods were available to us. Nevertheless, our results are of general significance for monitoring carnivore populations for conservation purposes. The prey biomass method can be used on carnivores that locally focus on a few easily censused prey species. Use of the average density method simply requires that there are sufficient studies on a given carnivore species to generate an average density figure. The home range method requires that one detailed study of demography and ranging behaviour is available. Finally, the interview method is limited to species that people recognize and that are sufficiently memorable to be reported on reliably. For this last method, individuals of the species must be either geographically localized in exclusive ranges or live in stable groups of various sizes so that different animals are identifiable. At least one of these methods is available for a large number of carnivore species. We encourage future researchers and managers investigating carnivore density to attempt to calibrate their methods, and where possible, to rely on more than one indirect approach.

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