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Abstract: A field-interview survey of the distribution and abundance of the cheetah *Acinonyx jubatus* was conducted in Kenya between May and September 1989, and June and August 1990. Two hundred and twenty respondents ranging from wildlife conservationists to traditional pastoralists gave precise descriptions of cheetah observations, including dates and locations of sightings, and number, age class, and sex of the cheetahs observed. The 369 detailed sightings collected consisted of 249 observations of all-adult groups and 120 observations of family groups. The average number of adults in all-adult sightings was 1·8 + SE 0·07, and the average litter size in family groups was 2·6 + SE 0·10. Density estimates across the country ranged from 0·009 to 0·102 cheetah km^{-2}, and were generally higher than elsewhere in Africa. A total number of 793 cheetahs was estimated in Kenya protected areas, and Masailand and the dry northern Districts appear to offer the best prospects for cheetah conservation in Kenya based on relative prey availability. The proportion of family groups among all sightings was twice as high in protected areas as on rangelands, and protected areas also held larger groups of males. The results do not support the thesis that cheetahs fare better on rangelands than in protected areas. Comparison with earlier surveys in Kenya showed remarkable stability in cheetah distribution and social structure over time. No firm conclusion could be drawn on trends in cheetah numbers, although scattered evidence supported a scenario of stability rather than decline in the last decades. Despite their limitations, interview based surveys can produce valuable results for monitoring elusive high-profile carnivores.

To Peter with compliments,
Paule

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Status of the cheetah *Acinonyx jubatus* in Kenya: a field-interview assessment

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Abstract

A field-interview survey of the distribution and abundance of the cheetah *Acinonyx jubatus* was conducted in Kenya between May and September 1989, and June and August 1990. Two hundred and twenty respondents ranging from wildlife conservationists to traditional pastoralists gave precise descriptions of cheetah observations, including dates and locations of sightings, and number, age class, and sex of the cheetahs observed. The 369 detailed sightings collected consisted of 249 observations of all-adult groups and 120 observations of family groups. The average number of adults in all-adult sightings was 1·8 + SE 0·07, and the average litter size in family groups was 2·6 + SE 0·10. Density estimates across the country ranged from 0·009 to 0·102 cheetah km^{-2}, and were generally higher than elsewhere in Africa. A total number of 793 cheetahs was estimated in Kenya protected areas, and Masailand and the dry northern Districts appear to offer the best prospects for cheetah conservation in Kenya based on relative prey availability. The proportion of family groups among all sightings was twice as high in protected areas as on rangelands, and protected areas also held larger groups of males. The results do not support the thesis that cheetahs fare better on rangelands than in protected areas. Comparison with earlier surveys in Kenya showed remarkable stability in cheetah distribution and social structure over time. No firm conclusion could be drawn on trends in cheetah numbers, although scattered evidence supported a scenario of stability rather than decline in the last decades. Despite their limitations, interview based surveys can produce valuable results for monitoring elusive high-profile carnivores.

Keywords: Cheetah; Conservation; Kenya; Status; Survey

1. Introduction

The current conservation status of the cheetah *Acinonyx jubatus* in Kenya is a controversial issue. Because cheetahs are elusive and typically roam over large home ranges, it is difficult to discern whether the species is actually rare or merely rarely seen, let alone if it has recently become scarce. Over the past 30 years, the fear that cheetah numbers could be declining in the country instigated several surveys of the cheetah's distribution and abundance (Graham and Parker, 1965; Myers, 1975; Hamilton, 1986). Unfortunately, these studies produced contradictory conclusions, and how cheetahs fare in Kenya today remains an open question.

Assessing the cheetah's status in Kenya is of particular significance for the species' conservation in Africa. In the last decades, cheetah numbers have drastically decreased throughout the Sahelian and Somalian regions under the combined pressures of desertification, rapid human population growth, and war (Le Houérou and Gillet, 1986; Newby, 1990). In southern Africa, the hostile attitude prevailing among livestock owners poses a serious threat to cheetah populations outside protected areas (Marker-Kraus and Kraus, 1990). In this context, investigating the persistence of healthy cheetah populations in their traditional East African strongholds of Kenya and Tanzania assumes particular importance.

Furthermore, well protected reserves may not be a universal panacea for the conservation of cheetahs. Cheetahs suffer alarmingly high cub mortality from lion and spotted hyena predation in the Serengeti National Park, Tanzania (Laurenson, 1995), and cheetah density in the Masai Mara National Reserve, Kenya, was found to be half that occurring on adjacent rangelands where large predator numbers are controlled by pastoralists

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(Burney, 1980). These results led to question the value of protected areas with large predator concentrations for cheetah conservation (Laurenson et al., 1992; Caro, 1994).

In this paper, I present the results of an extensive field-interview survey of cheetah distribution and abundance in Kenya, which provides a baseline for future monitoring of the species in the country. I also attempt to establish whether the cheetah's range has contracted over the last 30 years, and whether cheetah numbers are currently dwindling. Finally, I examine whether cheetahs appear to have better prospects on rangelands than in protected areas.

2. Methods

A field-interview survey appeared particularly suitable for ascertaining the status of the cheetah in Kenya. The species is popular and rare enough to make any encounter with a cheetah memorable, and the long-lasting associations of individuals within all-male (several years) and family groups (18 months) allow the differentiation of specific groups (Caro, 1994). Moreover, comparisons of carnivore densities derived from interview and long-term field studies showed that interview is a valid approach to surveying large carnivores provided that enough people are contacted and special care is taken to limit the most obvious pitfalls of the method (Creel and Creel, 1995; Gros et al., 1996).

Data were collected principally by means of detailed interviews with 131 people in Kenya. This method yielded reports of cheetahs in protected areas and on rangelands, including remote areas inhabited exclusively by traditional people. Fifty-six written questionnaires and 33 letters supplemented this data set. Interviews were conducted by driving to villages, farms, ranger outposts, and protected areas throughout the country to make direct contact with informants. The interview format was finalized during short field trips in May and June 1989, and interviews took place from July to September 1989 and June to August 1990. All regions of Kenya were surveyed except for the densely settled and farmed central and western highlands, the Turkana District, and the northeastern part of the country (Garissa, Mandera, Tana River and Wajir Districts) (see Fig. 1 for locations). Questionnaires and letters provided information about the two last regions. Respondents included wildlife administration staff (37), personnel of protected areas (35), farmers (33), researchers and conservationists (31), naturalists (22), traditional pastoralists (20), tourists (20), tour operators and guides (15), and professional hunters (7). Interviews were mostly conducted in English and Kiswahili, although I occasionally relied on local interpreters to translate my questions into tribal languages.

2.1. Interview questions

2.1.1. Cheetah sightings

Each respondent was asked to report all cheetah sightings that he/she could clearly remember. Each sighting location was pinpointed as precisely as possible by noting location name, name of most noticeable surrounding landmarks, and distance or travel time to

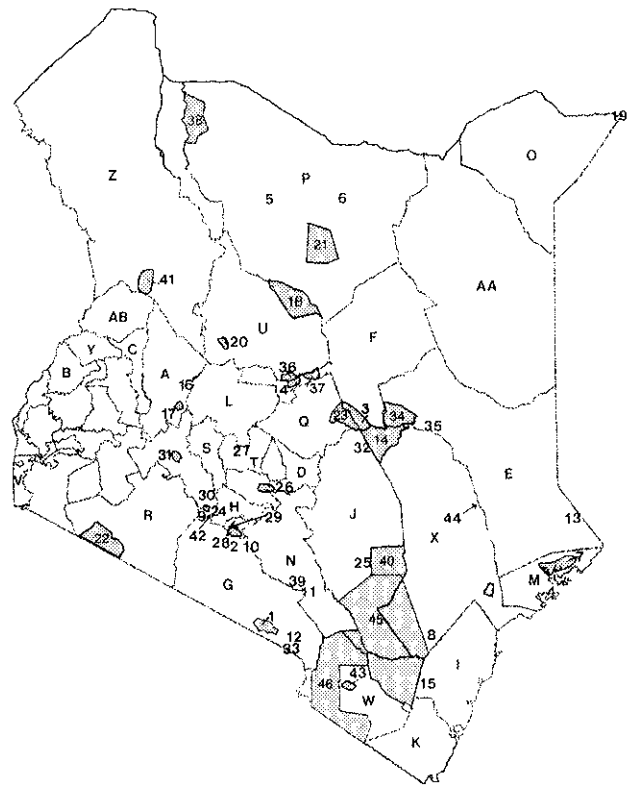

Fig. 1. Location of the geographic areas cited in the text. Shaded areas represent parks and reserves, and lines are Districts boundaries. 1. Amboseli National Park; 2. Athi plains; 3. Bisanadi National Reserve; 4. Buffalo Springs National Reserve; 5. Chalbi desert; 6. Dida Galgalu desert; 7. Dodori National Reserve; 8. Galana ranch; 9. Hell's Gate National Park; 10. Kapithi plains; 11. Kiboko ranch; 12. Kimana; 13. Kolbio; 14. Kora National Reserve; 15. Kulalu ranch; 16. Lake Baringo; 17. Lake Bogoria National Reserve; 18. Losai National Reserve; 19. Mandera town; 20. Maralal Game Sanctuary; 21. Marsabit National Reserve; 22. Masai Mara National Reserve; 23. Meru National Park; 24. Mount Longonot National Park; 25. Mutha; 26. Mwea National Reserve; 27. Mweiga; 28. Nairobi National Park; 29. Nairobi town; 30. Naivasha; 31. Nakuru National Park; 32. North Kitui National Reserve; 33. Oloitokitok; 34. Rahole National Reserve; 35. Saka; 36. Samburu National Reserve; 37. Shaba National Reserve; 38. Sibiloi National Park; 39. Simba; 40. South Kitui National Reserve; 41. South Turkana National Reserve; 42. Suswa; 43. Taita Hills Game Sanctuary; 44. River Tana; 45. Tsavo National Park (East); 46. Tsavo National Park (West). Districts: A. Baringo; B. Bungoma; C. Elgeyo-Marakwet; D. Embu; E. Garissa; F. Isiolo; G. Kajiado; H. Kiambu; I. Kilifi; J. Kitui; K. Kwale; L. Laikipia; M. Lamu; N. Machakos; O. Mandera; P. Marsabit; Q. Meru; R. Narok; S. Nyandarua; T. Nyeri; U. Samburu; V. South Nyanza; W. Taita-Taveta; X. Tana River; Y. Trans Nzoia; Z. Turkana; AA. Wajir, AB West Pokot.

settlements featured on a 1/1,000,000 map of Kenya (Philip and Son Ltd., London). More detailed regional maps and maps of protected areas were used when available. Locations where the respondent knew of the presence of cheetahs, without being able to remember a precise sighting, were also recorded. Both sorts of locations (400 in total outside protected areas) were used to derive a map of the cheetah's distribution in Kenya using the Arc Info Geographic Information System. For each reported sighting, the respondent was asked to specify the date of observation, the total number of cheetahs observed, the number and sexes of adults among them, the number of cubs, and the relative age of the cubs (age 1 = gray cub to jackal-sized cub, *c.* 2–6 months; age 2 = jackal-sized to 2/3 of adult size cub, *c.* 6–10 months; age 3 = 2/3 of adult size to full sized cub, *c.* 10–18 months (Caro, 1994)).

When interviewing traditional pastoralists, I first ascertained that there was no confusion about the cheetah as a species by asking for natural history details such as the description of the cheetah's hunting technique. Dates of past sightings were approximated using some important event in the life of the local community. Exact dates of these events, as well as locations where the cheetahs were seen were determined after the interview with the help of an educated member of the pastoralist group.

2.1.2. Trend in cheetah numbers

When people were known to have stayed more than 10 years in a given area, they were asked if they thought that the number of cheetahs had increased, remained stable, or decreased over time. In other studies, this type of question has yielded a high percent of 'decreasing' answers where species had independently been shown to experience a sharp decline (mountain gazelle, *Gazella gazella cora*, Margin and Greth, 1994; manatee, *Trichetus manatus manatus*, Reynolds and Szelistowski, 1994).

2.1.3. Cheetah-livestock interaction

To cast some light on the cheetah-livestock interaction, I asked traditional pastoralists and commercial farmers to quantify their livestock losses to cheetahs. I compared the demographic parameters of cheetahs in areas where respondents reported little or no cheetah depredation with those in areas where heavy depredation was reported. Furthermore, I asked respondents whether they killed cheetahs to protect their livestock or if they used alternative methods. This question was readily answered since law enforcement was virtually non-existent on remote rangelands. I compared demographic parameters in areas where cheetahs were killed as problem animals with those in areas where the species was reported unharmed.

2.2. Cheetah densities

2.2.1. Cheetah densities derived from interviews in nine study sites

Cheetah densities were estimated in nine study sites: Amboseli National Park, Masai Mara National Reserve, Meru National Park, Nairobi National Park, Samburu–Buffalo Springs National Reserve, Taita Hills Game Sanctuary, Lake Bogoria National Reserve, a subset of Laikipia ranches, and a subset of the ranches of the Nakuru-Naivasha region (Fig. 1). I used two methods of estimating cheetah density for each site. First, respondents were asked to estimate the minimum and maximum number of cheetahs in the study site. Averages for each value were subsequently calculated and divided by area. Second, density was calculated by dividing the total number of cheetahs reported in sightings made in 1990 by the area of the site of interest. Sightings that were similar in group size and composition to another group of cheetahs already described were discarded. For example, if a group of three males had been observed in the area of interest, any additional observation of three adults or three cheetahs during 1990 would not be considered. Obviously, there could be more than one group of a given composition in an area. Moreover, individuals temporarily separate from their group. Finally, family groups eventually separate and male coalitions sometimes break up (S. Durant, pers. comm.). Despite numerous potential sources of error, this second method provides reasonably accurate results (Gros et al., 1996). Sizes of protected areas were taken from the literature (IUCN, 1987). Laikipia ranches area was derived by adding up areas of the farms visited, and the area of the Nakuru-Naivasha region was approximated from its almost rectangular dimensions on a map of Kenya (Kenya, 1:1,100,000, Nelles Verlag).

2.2.2. Estimate of total number of cheetahs in protected areas in Kenya

I could not compute cheetah density from interview returns outside of the nine study sites because the number of sightings per area was not high enough. I therefore estimated the total number of cheetahs in the protected areas of Kenya using the average density method (Gros et al., 1996). Estimates of cheetah densities, which are mostly informed guesses by experienced field researchers, are available for 14 protected areas in Africa outside Kenya (Gros et al., 1996). Averaging these estimates results in a mean density of one cheetah per 47 km^2 (i.e. 0·021 cheetah km^{-2}). I estimated the number of cheetahs present in Kenyan protected areas by adding up the areas of all parks and reserves where cheetahs were found to occur in this survey, and multiplying the total obtained by 0·021 cheetah km^{-2} (Table 1). The accuracy of my estimate of the total number of cheetahs in Kenya protected areas hinges on

Table 1
Estimates of cheetah numbers in Kenya protected area and in two ranching regions

Protected areas	Area in km²	Number of cheetahs (nearest integer)	
		Average method	Interview method
Tsavo NP	20820	440	na
Marsabit Biosphere Reserve	2088	44	na
S Kitui NR	1833	39	na
Kora NR	1788	38	na
Losai NR	1807	38	na
Sibiloi NP	1570	33	na
Masai Mara NR	1510	32	38
Rahole NR	1270	27	na
S Turkana NR	1091	23	na
Meru NP	870	18	27
N Kitui NR	745	16	na
Bisanadi NR	606	13	na
Amboseli NP	392	8	7
Samburu-Buffalo Spring NR	296	6	19
Shaba NR	239	5	na
Lake Nakuru NP	157	3	na
Lake Bogoria NR	107	2	na
Maralal Game Sanctuary	113	2	na
Nairobi NP	117	2	11
Taita Hills Game Sanctuary	113	2	9
Hell's Gate NP	68	1	na
Mwea NR	68	1	na
Total in protected areas	37668	793	113
Laikipia ranches	5209	na	91
Nakuru–Naivasha ranches	3715	na	36

na = not available; NP = National Park; NR = National Reserve.

the quality of cheetah density estimates used to compute the mean cheetah density in protected areas. It also depends on the ecological resemblance between the 14 protected areas of reference and the parks and reserves of Kenya. Previous comparisons showed that estimates of cheetah densities obtained by the average density method ranged from 21 to 143% of the densities derived from long term field studies in three East African protected areas (Gros et al., 1996). I used these percentages to provide minimum and maximum boundaries to the total number of cheetahs estimated.

2.2.3. *Maximum potential number of cheetahs in Kenya*

I derived an estimate for the maximum potential number of cheetahs in Kenya from the biomass of medium-sized herbivores, available on a district to district basis for the 1977–1985 period (Peden, 1984; Mbugua, 1986) (Table 2). The average density method could not be used to predict the total number of cheetahs in the country due to lack of information on cheetah densities in Africa outside of protected areas. Previous research showed that cheetah biomass and prey biomass of herbivore weighing 15 to 60 kg are significantly

Table 2
Maximum potential number of cheetahs in Kenya districts based on prey biomass alone

Districts	Area (km²)	Prey biomass (kg km^{-2})	Maximum potential number of cheetahs (nearest integer)
Narok	16115	382·19	2514
Marsabit	73952	25·89	1142
Wajir	56501	31·91	1006
Kajiado	19605	113·71	982
Isiolo	25605	65·57	796
Turkana	61768	19·19	790
Garissa	43931	15·47	498
Laikipia	9718	106·37	459
Tana River	38694	11·44	377
Taita-Taveta	16959	31·15	297
Samburu	17521	20·76	235
Kitui	29388	3·96	199
Mandera	26470	2·02	159
Kwale	8257	16·91	98
Kilifi	12414	6·37	96
Baringo	9885	4·96	71
West Pokot	9090	0·47	49
Lamu	6506	0·78	36
Total	482379		9804

correlated ($y = 0{\cdot}015x + 0{\cdot}1983$, $r^2 = 0{\cdot}63$, $p < 0{\cdot}01$, where x represents prey biomass and y cheetah biomass, both in kg) (Gros et al., 1996). The figure that I estimated represents the number of cheetahs that would be found in Kenya districts provided that no factors other than prey density were limiting cheetah population sizes. The accuracy of this figure depends on the quality of the prey and cheetah biomass figures used to build the regression model, and of the prey biomass used as predictor of potential cheetah numbers. Additional error may stem from possible changes in herbivore biomass occurring between the period 1977–1985 and the present, and from the fact that cheetahs occur in parts rather than the whole of each district. Finally, no biomass data was available for Embu, Meru, Machakos and Nakuru Districts where cheetahs were commonly reported in 1990, nor for some other districts where the species was seldom seen (Hamilton, 1986; this study).

2.3. *Average group sizes and cub-to-adult ratios*

Adult male cheetahs live either alone or in permanent male groups, while females are solitary if not accompanied by a litter. Sub-adult litter-mates remain in temporary groups after they separate from their mother (Caro, 1994). To account for all these types of association, I computed the number of adult cheetahs in all-adult sightings (referred to as number of adults), the number of cubs within family groups (litter size), and the total number of individuals per sighting (total group

size). The last measure allowed me to include in the analysis sightings reporting only total numbers of cheetahs observed. Average number of adults, litter size, total group size, and cub-to-adult ratio (the total number of cubs reported in all sightings divided by the total number of adults in all sightings) were calculated for the country as a whole. The same parameters were also computed for individual regions and individual protected areas to analyze spatial variation in group size and to compare grouping patterns inside and outside protected areas. For these purposes, Kenya rangelands were divided into seven regions on the basis of climate and landuse (Table 3).

2.4. Comparison with Graham and Parker's 1965 cheetah survey

Graham and Parker (1965) conducted a cheetah survey based on interviews and correspondence with 205 people between October 1964 and March 1965. They obtained 1225 sightings of cheetahs in East Africa (Kenya, Tanzania and Uganda), 658 of which were from Kenya, but did not present their findings on a country by country basis. Nevertheless, they stated that grouping patterns of adults and the proportion of sightings composed of adults vs sightings of family groups outside protected areas in Kenya were 'close to the overall average' obtained by lumping all sightings over East Africa. Since the borders between the three East African countries do not reflect any ecological discontinuity and the entire region was administrated under the same colonial rule until 1963, it seemed appropriate to compare the results of my Kenyan survey to theirs of East Africa.

2.5. Limitations of the survey method

Attempting to assess a species' status on the basis of sighting reports has limitations. Respondents can affect the results with problems originating from poor memory and incorrect determination of number, sex, or age of the cheetahs at time of observation; for example, large cubs can easily be mistaken for adults. The perceived necessity to provide an answer regardless of one's actual knowledge may be a further source of error. To minimize some of these problems, I generated as large a data set as possible for each area surveyed in order to corroborate information. I also stressed to each respondent that 'I do not know' was a perfectly acceptable answer to any of the questions. Because reliability is a major concern in biological surveys based on interviews, particular effort was made to address this issue. I reviewed interviews at the end of each day, discarded doubtful information, and assigned the remaining interviews a four point reliability score as follows: one point for the precision of sightings described (in terms of date, location, number of cheetahs, composition of the group); one point when no wrong or doubtful information was given (such as: sexing cheetahs from a long distance); one point for the consistency of the information provided (consistency was checked by asking the respondent to restate specific details he/she had provided earlier during the interview); and one point if the respondent was co-operative, interested, and concentrated during the interview. Analyses were run both on the whole data set and using only data with reliability scores of three and four. No substantial differences were found, and the results presented below are based on the analysis of the whole data set.

3. Results

3.1. Current distribution of the cheetah in Kenya

Specific locations of all 400 cheetah observations I collected outside of protected areas and all the protected areas within which I obtained cheetah reports are shown in Fig. 2. This distribution map should be interpreted as a conservative representation of the species' current range. Blank areas do not necessarily signify the cheetahs' absence, but simply that no sightings were reported there. Furthermore, although regions where interviews were conducted tend to have more cheetah reports than those for which only written accounts were obtained (Turkana District and Eastern Region), it is difficult to

Table 3
Division of the cheetah range into seven regions based on climate and landuse

Region	Climate	Landuse	Geographic scope
Marsabit	Very arid	Nomadic camel pastoralists	Marsabit
Eastern region	Arid to very arid	Nomadic cattle pastoralists	Garissa, Mandera, Tana River, and Wajir
Samburu	Arid	Nomadic cattle pastoralists	Samburu, Isiolo, Baringo, and West Pokot
Tsavo surroundings	Semi-arid to arid	Commercial cattle ranchers	Ranches adjacent to Tsavo National Park
Masailand	Non-arid to arid	Nomadic cattle pastoralists	Kajiado and Narok
Laikipia	Non-arid	Commercial cattle ranchers	Laikipia
Nakuru	Semi-arid	Commercial cattle ranchers	Ranches between Nakuru and Hell's Gate National Parks

Climates zones are from Ominde, 1971; geographic areas are Districts if not otherwise specified.

weigh the relative influence of each method on the resulting distribution map. Given these shortcomings, the map is intended as a basis for future monitoring of the species in Kenya rather than a complete assessment of current cheetah distribution in the country.

3.2. Comparison with previous accounts of cheetah distribution

My map of cheetah observations closely resembles three previously published cheetah distribution maps

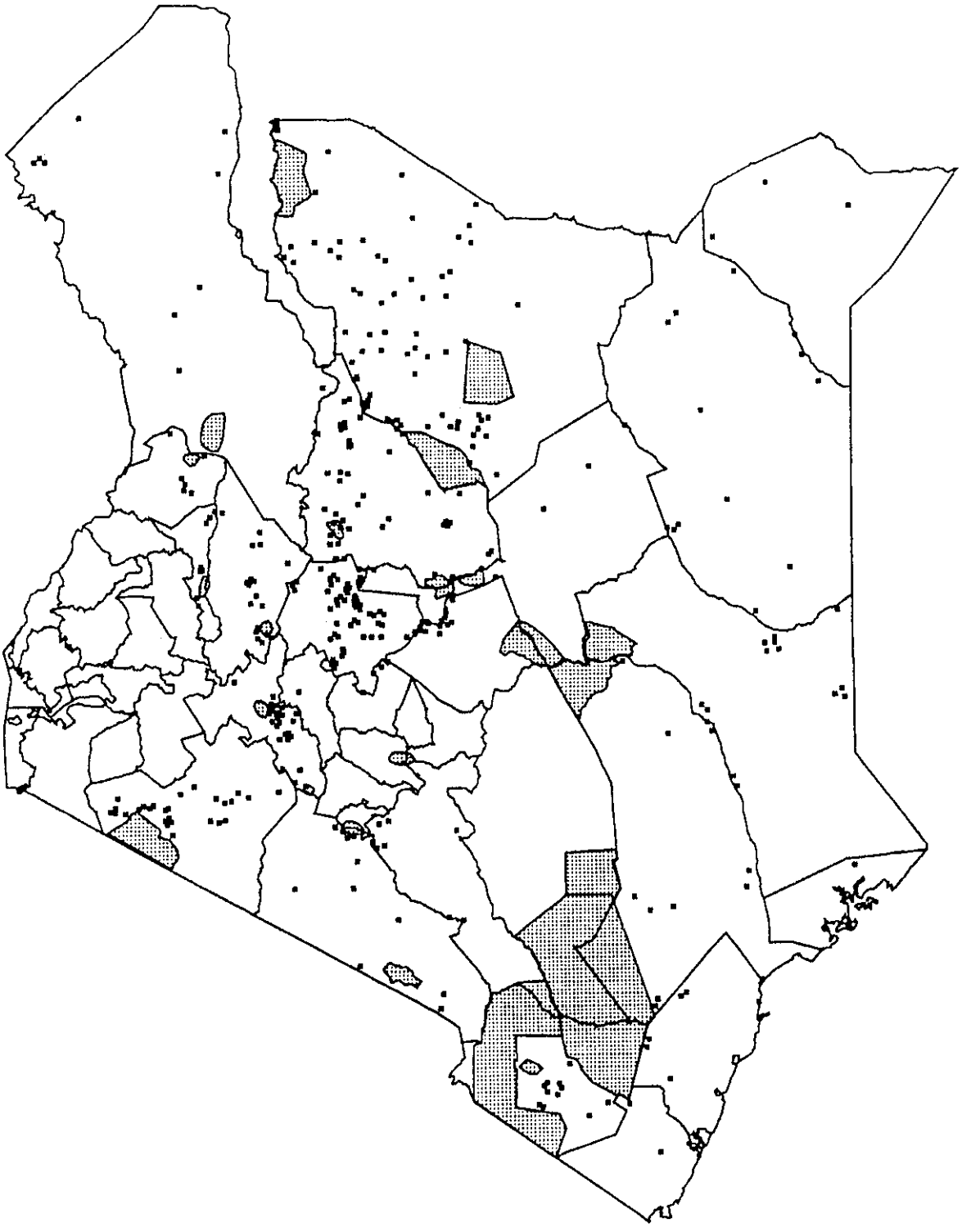

Fig. 2. Locations of cheetah sighting reports. Cheetah sightings reported outside of protected areas are indicated by dots. Protected areas where cheetah presence was documented are featured in shaded grey. (See Appendix for information about sightings of cheetahs within protected areas).

Table 4
Areas included in this survey but not unanimously considered as part of the cheetah range in previous works (Stewart and Stewart, 1963; Graham and Parker, 1965; Myers, 1974; Hamilton, 1986)

Area	Date of survey					
	1963	1965	1974	1978	1986	This survey
Chalbi desert	-	-	x	-	?	x
Dida Galgalu area	-	x	x	x	?	x
Dodori area	-	x	-	-	?	x
Along the Tana river	x	x	-	-	?	x
Kitui District	-	x	?	-	x	x
Central highlands	-	x	?	-	x	x
Elgeyo-Marakwet District	?	-	-	-	x	x
Nyandarua District	-	-	-	-	x	x
Baringo District[a]	?	-	-	x	?	x

x = included in the cheetah's range by the author of the survey; - = excluded; ? = unknown.
[a] excluding the Baringo–Bogoria lakes area.

(Stewart and Stewart, 1963; Graham and Parker, 1965; Kingdon, 1977), especially that of Graham and Parker who used interview and mapping methods very similar to mine. The 1990 results also confirm cheetah presence in all the regions cited by Myers (1975), and in 24 of 29 districts included in Hamilton's (1986) assessment of the cheetah's range. However, a number of locations for which I obtained cheetah sightings were not reported by other authors (Table 4). Conversely, I did not collect any sighting for a few locations where cheetahs had been reported previously. These are Kolbio South of Garissa District (Graham and Parker, 1965), Mweiga in Nyeri District (Graham and Parker, 1965), the surroundings of Mandera town (Myers, 1975), and the districts of Bungoma, South Nyanza, Trans Nzoia, and Kiambu (Hamilton, 1986) (see Fig. 1 for locations). Finally, there are areas for which the number of cheetah reports was lower in this survey than in the previous studies. Graham and Parker's map features a larger number of cheetah sightings in the Kapithi Plains, in the Kajiado District, in the region bordering the Tana River between its mouth and Saka, and in the vicinity of Mwea (Embu), Mutha (Kitui) and Simba (Machakos). Moreover, Stewart and Stewart (1963), Myers (1975), and Kingdon (1977) all included sizable areas of Turkana District in their cheetah distribution maps, whereas I gathered only eight sightings for the whole district.

3.3. Trends in cheetah numbers over the last 10 years

Sixty two per cent of the 122 responses indicated either no change (42·6%) or an increase (19·7%) in cheetah numbers over the last 10 years in the area for which respondents were giving information.

3.4. Analysis of sightings

The survey yielded 482 sightings of cheetahs, 88% of which were made between 1985 and 1990. A detailed description was obtained for 369 of these sightings. Two hundred and forty-nine were composed of adults only (134 lone individuals, 66 pairs, 30 trios, 15 quartets, and 4 larger groups) and the remaining 120 were sightings of family groups (162 adults and 308 cubs). Average litter size was 2·6 + SE 0·10 (Table 5), which falls within the range of litter sizes reported from detailed field studies in East Africa (2·5 cubs accompanying their mother in Masai Mara (Burney, 1980) and approximately two in Serengeti (Laurenson, 1992)). Average number of adults was 1·8 + SE 0·07, and average total group size 2·4 + SE 0·06.

3.5. Estimates of cheetah abundance

3.5.1. Cheetah densities in the nine study sites

Estimates of cheetah densities were obtained for 7 protected areas and 2 cattle ranching regions (Table 1, Appendix 1). Previous assessment of cheetah density was available for two of the protected areas: Nairobi National Park and Masai Mara National Reserve. No change in density was detected in Nairobi National Park where I estimated 0·094–0·102 cheetah km^{-2}, which closely matches McLaughlin's (1970) result (0·094 cheetah km^{-2}). In Masai Mara National Reserve, however, I obtained a higher cheetah density estimate than Burney's (1980): 0·022–0·027 km^{-2} vs 0·014 km^{-2}.

Table 5
Breakdown of cheetah litters reported in this survey by size and age

Relative age of litter	Number of cubs per litter						Number of litters	Average litter size
	1	2	3	4	5	>5		
Age 1	25·0	25·0	25·0	10·0	10·0	5·0	20	2·7
Age 2	15·4	38·5	15·4	15·4	15·4	0·0	13	2·8
Age 3	27·0	27·0	34·6	7·7	3·8	0·0	26	2·3
Age unknown	13·1	44·3	24·6	11·5	4·9	1·6	61	2·6
All ages	18·3	36·7	25·8	10·8	6·7	1·7	120	2·6

Decimal figures are percentages

Estimates of cheetah densities were available for 14 protected areas in Africa outside Kenya, and ranged from 0·002 to 0·057 km^{-2} (Gros et al., 1996). Cheetah densities were higher in all Kenyan protected areas examined than in 9 of the 14 protected areas elsewhere in Africa. Finally, I found a non significant trend towards a correlation between cheetah density and cub-to-adult ratio across my nine study sites ($r_s = 0{\cdot}623$, $n = 8$, $p = 0{\cdot}099$), whereas cheetah density was clearly not correlated with litter size ($r_s = 0{\cdot}289$, $n = 8$, $p > 0{\cdot}1$) nor with adult group size ($r_s = 0{\cdot}144$, $n = 8$, $p > 0{\cdot}1$).

3.5.2. Number of cheetahs in protected areas in Kenya

I documented cheetah presence in 23 protected areas covering 37,668 km^2 (Table 1). Using the average density method, the total number of cheetahs within protected areas in Kenya was estimated to be 793 individuals. Boundaries for this estimate, derived from maximum percent of discrepancy between average method estimates and densities from long term field studies, were 167 and 1134.

3.5.3. Maximum potential number of cheetahs in Kenya

Using the cheetah-prey biomass regression model, I obtained a maximum potential number of 9804 cheetahs for the whole country. Totals per district are given in Table 2. Obviously factors other than prey density, such as competition with other large carnivores, disease, and killing by pastoralist herdmen and commercial farmers, are likely to limit cheetah population sizes. Unfortunately, the influence of each potential limiting factor has not yet been quantified. Therefore, the figures estimated should be considered as indicators of the relative potential of Kenya subregions for cheetah conservation, rather than interpreted as reflections of real numbers of cheetahs in the field.

3.6. Comparison of the results inside and outside of protected areas

The percentage of observations including cubs was twice as high (Mann-Whitney U test; $U = 7{\cdot}5$, $p = 0{\cdot}013$) inside protected areas (27·4%, $n = 9$) than outside (14·3%, $n = 7$). Nevertheless, litter sizes did not differ significantly ($U = 22{\cdot}5$; $p > 0{\cdot}1$) inside (2·2, $n = 9$) and outside of protected areas (2·8, $n = 7$), nor did cub-to-adult ratios (1·9, 2·0 respectively; $ns = 502$, 402 cheetahs; $\chi^2 = 0{\cdot}1$; $p > 0{\cdot}1$).

There was no significant difference in total group size ($U = 56$, $p > 0{\cdot}1$) whether the observations were made in protected areas (1·9, $n = 18$) or on rangelands (2·4, $n = 7$). Males observed inside protected areas were more likely ($\chi^2 = 5{\cdot}5$; $p = 0{\cdot}019$) to be in a group than were those seen on rangelands: males were observed in a group in 54% of all-male sightings inside protected areas vs 25% outside. In contrast, adult group sizes tended to be somewhat larger ($U = 29$, $p = 0{\cdot}092$) outside of protected areas (1·7, $n = 7$) than inside (1·2, $n = 15$).

Evaluations of trends in cheetah numbers were similar ($\chi^2 = 0{\cdot}2$, $p > 0{\cdot}5$) whether people were referring to protected areas or to rangelands: 60% of 47 answers reported a stable or increasing trend inside protected areas vs 64% of 75 answers outside.

3.7. Cheetah–livestock interaction

On rangelands where livestock owners acknowledged killing cheetahs 65% ($n = 20$) of the reports described cheetah populations as decreasing vs 36% ($n = 22$) in areas where people claimed not to harm the species ($\chi^2 = 3{\cdot}4$; $p = 0{\cdot}064$). In addition, small groups of cheetahs were more commonly reported ($\chi^2 = 3{\cdot}9$; $p = 0{\cdot}047$) in areas of cheetah–livestock conflict than in areas of no conflict (77% and 52% of groups with less than three cheetahs, respectively; $n = 52$, 19), and the proportion of small litters (i.e. litters of 1 or 2 cubs) was larger in problem areas than in areas where no conflict existed (9 out of 17 litters vs 0 out of 7 litters; Fisher exact test; $p = 0{\cdot}022$).

3.8. Comparison with Graham and Parker's 1965 survey

Thirty-three percent of the cheetah sightings ($n = 369$) reported in this survey were of family groups, vs 21% ($n = 1225$) in Graham and Parker's survey ($\chi^2 = 22{\cdot}3$, $p < 0{\cdot}001$). The cub-to-adult ratio was likewise significantly higher ($\chi^2 = 28{\cdot}6$, $p < 0{\cdot}001$) in the 1990 survey (0·51, $n = 910$ cheetahs) than in the 1965 survey (0·33, $n = 2785$). There was no difference ($\chi^2 = 4{\cdot}7$; $p > 0{\cdot}1$) in the relative proportions of single adult, pair, trio, quartet, and groups of more than four adults observed in the two surveys (972 sightings of adult cheetahs in 1965, 249 sightings in 1990). Similarly, the proportion of litter sizes of 1, 2, 3, 4, and more than four cubs were comparable ($\chi^2 = 5{\cdot}0$; $p > 0{\cdot}1$) in the two surveys (252 litters in 1965, 120 litters in 1990).

4. Discussion

4.1. Changes in the cheetah's distribution and abundance

A comparison of the findings of the 1990 cheetah survey with five earlier accounts of the species' distribution in Kenya (Stewart and Stewart, 1963; Graham and Parker, 1965; Myers, 1975; Kingdon, 1977; Hamilton, 1986) shows a remarkable stability of the cheetah's range over the last 30 years. Authors unanimously include a core of 17 districts of Kenya in the cheetah's range (Fig. 3). Discrepancies arise with regard to certain specific localities within the core distribution and whether to include additional small peripheral districts.

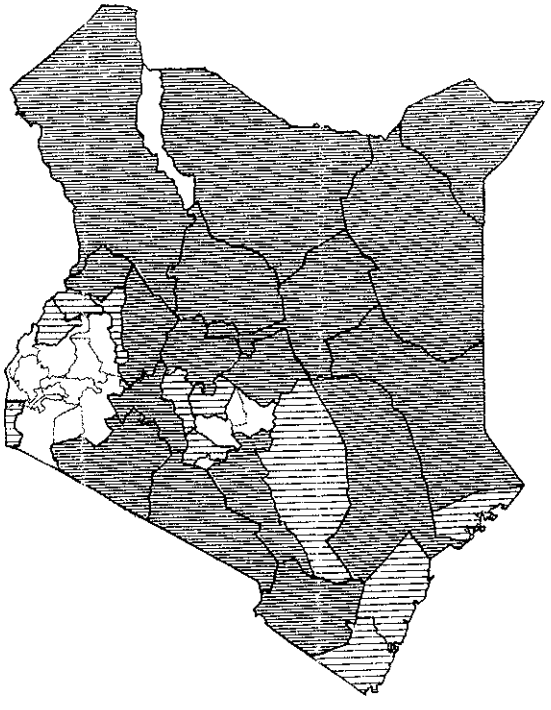

Fig. 3. Agreement and discrepancies between the six assessments of the cheetah's distribution in Kenya for the 1963–1990 period. Dense fill pattern indicates the Districts included in the cheetah range by all six authors. Loose fill pattern indicates controversial Districts, those that only some authors included in the cheetah's range. White indicates Districts not included in the cheetah distribution by any author.

Some of these discrepancies can be attributed to the variety of survey methods employed. For example, surveys reporting the exact locations where cheetahs were seen tend to produce more precise but less comprehensive maps than those based on presence or absence of the species within arbitrarily defined geographic units such as districts. Even when comparable methods are used, unequal search effort between surveys may generate spurious differences in distribution. Nevertheless, most of the controversial areas are close to the edge of the species' core distribution in the country, and authors who claimed cheetah presence there reported small populations. Since there is no obvious trend towards local extinction of cheetahs in any of these places (i. e. recent surveys do not seem to exclude any of these areas more frequently than former works did, see Table 4), I suggest that these controversial areas could be marginal biotopes in which cheetahs maintain permanent but sparse populations, or localities that are periodically recolonized by cheetahs when favorable conditions prevail.

Although no major change could be detected in cheetah distribution in Kenya since 1963, it cannot be inferred that the number of cheetahs in the country has remained constant over time, because changes in densities can occur within a stable geographical range. Direct comparison of current and past cheetah densities was possible for only two protected areas: Nairobi National Park where cheetah numbers seem to have been stable since 1970 (McLaughlin, 1970) (see Appendix 1), and Masai Mara National Reserve for which I found a higher cheetah density than Burney (1980). Additional comparisons suggest stability or increase of cheetah numbers in the country. First, cheetah density was shown to be positively correlated with cub-to-adult ratio, a parameter that was greater in this survey than in Graham and Parker's (1965) study. Second, it has been suggested that disruption of social organization could either cause or reflect the decline of a wildlife population (Poole, 1989; Young and Isbell, 1994). However, the grouping patterns of adult cheetahs and the relative proportion of litters of different size were similar in this survey and in Graham and Parker's. Third, 62% of the respondents thought that cheetah numbers had increased or remained stable in the last 10 years in the region for which they were providing information. Yet, I collected fewer cheetah reports than Graham and Parker's in several regions of Kenya, and my cheetah sightings for Turkana District were very scant. This could reflect local declines in cheetah densities but could also result from differences in sampling effort. Thus most available information points to stability or an increase in cheetah numbers in Kenya in the last 10–30 years. Nevertheless, one could imagine scenarios of decreasing cheetah numbers in Kenya that would be consistent with the results I obtained. For example, increased adult mortality, provided it affects males slightly more than females, would produce a higher cub-to-adult ratio and a larger proportion of sighting with cubs, but nonetheless lead to a decrease in total cheetah density. Therefore, although the reported distribution of the cheetah in Kenya has remained mostly stable since 1963, and despite indirect evidence for little change in density over time, firm conclusions on the dynamics of cheetah numbers in the country cannot be drawn at this stage.

4.2. Number of cheetahs in protected areas in Kenya

I estimated a total of 793 cheetahs in protected areas in Kenya using the average density method. Estimates obtained by that method were lower or equal to those obtained by the interview method in five out of the six protected areas for which both types of estimates were available, and only slightly higher in the last area (Table 1). Since the interview methods itself tend to underestimate actual cheetah densities (Gros *et al.*, 1996), 793 is probably a conservative estimate of cheetah numbers in Kenya protected areas.

Interestingly, 55% of the total number of cheetahs estimated in protected areas in Kenya was generated by Tsavo National Park alone (Table 1). Although the 440 cheetahs predicted for this park could be an overestimate of the real population size, it is likely that Tsavo's population is the largest of all cheetah populations

found within protected areas in Kenya. Tsavo National Park is so large that, even when using the lowest cheetah density documented in protected areas in Africa (0·0021 cheetah km^{-2}; Gros *et al.*, 1996), one still obtains a population of 44 cheetahs, as high as the next best area. Relatively large cheetah populations were also predicted for other vast protected areas of the driest part of the country not renowned as important cheetah refuges, such as Kora, Marsabit, or Losai National Reserves (Table 1). Hence my results highlight the importance of large dry protected areas for cheetah conservation, and confirm that protected areas with large seasonal concentration of herbivores, such as Masai Mara National Reserve and Samburu-Isiolo complex (Appendix 1), also have a key role to play in the cheetah's survival in Kenya. Nevertheless, my estimates also suggest that all protected populations, except perhaps that of Tsavo National Park, are too small to be viable (Shaffer, 1987). Therefore, protecting cheetah populations both in protected areas and on their surrounding rangelands seems necessary to insure the long term survival of the species in Kenya.

4.3. Regions offering the best prospects for cheetah conservation in Kenya

My estimates of maximum potential number of cheetahs per district can be interpreted in terms of relative importance of the regions of Kenya for cheetah conservation. Masailand, which represents only 7% of the total estimated cheetah range in Kenya, accounted for 35·6% of the total potential cheetah number in the country. This result was mostly due to the very large potential prey biomass in Narok district. The dry northeastern part of the country claimed roughly an equally large part of the total potential cheetahs (40·6%) spread throughout 58% of the total cheetah range. Estimates for Turkana District were lower than in other dry districts of comparable size, i.e. Marsabit and Wajir Districts. This suggests that human pressures, most likely subsistence hunting, must have contributed to reduce prey biomass in Turkana District. It also supports my hypothesis, derived from distribution data, that cheetah numbers had declined in Turkana district in the recent past. Laikipia and, to a lesser extent, Taita Taveta Districts achieved moderate potential numbers of cheetahs due to high prey biomass rather than size. Other districts of Kenya could support only small cheetah populations.

Clearly, prey density is not the only ecological factor affecting cheetah densities, and more research on the quantitative effect of human activities on cheetah populations is needed before precise estimates of cheetah numbers outside of protected areas in Kenya can be produced. Nonetheless, on the basis of my results, I agree with Hamilton (1986) that Myers' (1975) prediction that no more than 1200 cheetahs would remain in the country by 1980 was probably too pessimistic.

4.4. Cheetah status inside versus outside protected areas

The idea that rangelands might offer a better option for conserving cheetahs than the classical setting of protected areas (Laurenson *et al.*, 1992) stems from the discovery of a very high cub mortality due to lion predation in the Serengeti National Park, Tanzania (Laurenson, 1992). Additional support for this argument comes from thriving populations of cheetahs on communally owned rangelands in the Mara region in Kenya (Burney, 1980) and on cattle farms in southern Africa (Wilson, 1987; Morsbach, 1986). Are those situations exceptional or do they reflect a general advantage of rangelands over protected areas for the conservation of cheetahs?

Comparing the demographic parameters of protected cheetah populations with those of rangeland populations throughout Kenya indicated better status in protected areas. Where cheetah densities could be computed, they were generally higher in protected areas (Table 1). Although there was no difference in total group size, litter size, cub-to-adult ratios, or trends in cheetah numbers inside and outside protected areas, the proportion of females with cubs was twice as high in protected areas suggesting that these protected areas act as centers for cheetah reproduction. Females raising cubs may seek protected areas, which typically contain a higher density of prey than rangelands, at a time when their nutritional requirements are high. Interestingly, lone females were also more likely to be found inside protected areas than outside, though this result is based on only 24 reports. Moreover, the proportion of male groups, which have a higher competitive ability than single males for holding territories in female rich areas (Caro, 1994), was also higher in protected areas than outside.

Although cheetahs living on rangelands are often relieved from the pressures of heavy predation by lions, interspecific competition at kills, and harassment by tourist vehicles, they yet have to cohabit with livestock farmers and pastoralist people. As could have been expected, reports of declining cheetah populations were more common where farmers acknowledged killing cheetahs, providing evidence that the degree of success of cheetahs on Kenyan rangelands partially depends on the attitude of livestock owners.

In short the cheetah populations of Kenya rangelands, considered as a whole, do not seem to fare better than those living in the country's parks and reserves. This does not preclude the possibility of finding higher cheetah densities outside of some particular reserves than within those reserves, as Burney (1980) did in Masai-Mara. Cheetah density should be higher on rangelands with ecological characteristics similar to those in

adjacent protected area (particularly with a sizable prey base), but, with lower concentrations of large carnivores. This combination of factors, however, does not seem to occur frequently enough to foster higher cheetah status on rangelands at the scale of the country. However, the most appropriate design to test for a 'rangeland advantage' and for the conditions under which it occurs would be to compare cheetah demographic parameters in a number of pairs of protected areas and adjacent rangelands. Unfortunately, such data are not available for Kenya. Although cheetah density and certain reproductive parameters appear overall lower outside parks and reserves than in protected areas, the majority of the cheetahs of Kenya live outside protected areas, due to the low ratio (<8%) of protected to unprotected lands within the cheetah range. Conserving cheetahs on rangelands is essential in order to maintain large effective population sizes and to assure connection between protected populations.

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APPENDIX

Cheetah populations of some protected areas and rangelands in 1990

Nairobi National Park
Minimum population—a female and three subadult cubs, a female and four cubs born March–April 1990, a pair of males. Density—average of respondents' estimates (11–12) cheetahs, 0·094–0·102 cheetah km^{-2}, highest density in a protected area in Africa. Comparison with Graham and Parker 1965 study—no change in average total group size, adult group size, litter size, nor cub-to-adult ratio between 1965 and 1990 data; higher proportion of cheetah sightings including cubs in 1990 ($x = 68\%$, 39%; $n = 19$, 69; $\chi^2 = 5{\cdot}155$, $df = 1$, $p < 0{\cdot}025$). Trend—Stable. Typically 1–2 males and 1–2 family groups (3–5 cubs) in the park (Foster and Kerney, 1967; McLaughlin, 1970; Eaton, 1974). Neighbouring cheetah locations—Athi plains, estates in Langata and Embakasi areas. Little cheetah depredation complaints (Capture Unit Warden, pers. comm.).

Amboseli National Park
Minimum population—a female and two cubs, an adult, a pair of males. Density—average of respondents' estimates: 5–8 cheetahs, 0·013–0·02 cheetah km^{-2}. Comparison with Graham and Parker (1965) study—lower proportion of sightings including cubs in 1990 vs 1965 ($x = 28{\cdot}5\%$, 50% respectively, $n = 18$, 72, $\chi^2 = 4{\cdot}521$, $df = 1$, $p < 0{\cdot}05$); highest cub-to-adult ratio in East Africa in 1965 (0·49) vs among lowest in Kenya protected areas in 1990 (0·40). Trend—decrease in numbers since 1975–1980, possibly due to harassment by tourists (Mr Kioko, ex-warden in Amboseli, J. Poole, D. Dames, pers. comm). Circumstantial evidence: at least 10 cheetahs (a female and two cubs, a female and three cubs, a pair of males, an adult male) observed regularly during three months of cheetah photographic work in 1980 (D. Renn, pers. comm.); no cheetah found in the park by same professional photographer in 1993. Neighbouring cheetah locations—an adult male between Buffalo lodge and the park gate, solitary individuals next to Kimana in 1993 (D. Renn, pers. comm.).

Masai Mara National Reserve
Minimum population—*Northwest*: a female and two subadult cubs (by middle of 1990), and a pair of males around Kichwa Tembo, Governor's Camp and Musiara; a female and three cubs in Musiara (December 1990); an adult around Kichwa Tembo all year. *Southwest*: a resident female west of the Enkipai river next to Tanzania border. *Central* region: two adults around Keekorok; a male in the Metha plains; at least one female in Posee/Talek area. *Northeast*: three adult males next to Sekenani river; a female and subadult male cub next to Mara Sarova lodge. *Southeast*: a female with two very young cubs by September 1990 next to Olempito hills, a female with four very young cubs next to Ololoitikoishi. A four-adult-male group in reserve. Density—average of respondents' estimates: 34–42 cheetahs, 0·022–0·028 cheetah km^{-2}. Comparison between 1980 (Burney, $n = 61$ cheetahs) and 1990 (this study, $n = 32$ cheetahs)—1990 density twice 1980's (0·014 cheetah km^{-2}); no difference in total group size (2·1 vs 2·4, $\chi^2 = 0{\cdot}127$, $p > 0{\cdot}05$), adult group size (2·2 vs 2·4, $\chi^2 = 0{\cdot}318$, $p > 0{\cdot}05$), litter size (1·5 vs 1·8, *Fisher* $= 0{\cdot}37$, $p > 0{\cdot}05$), nor cub-to-adult ratio (0·65 vs 0·57, $\chi^2 = 0{\cdot}081$, $p > 0{\cdot}05$). Trend—stable or increasing (89% of responses, $n = 9$).

Samburu (165 km^2), *Buffalo Springs (131 km^2) and Shaba (239 km^2) complex*
Minimum population January–October 1990—Samburu NP/Buffalo Springs NR: a pair of males, a female and two young, a female and four nearly mature offspring, an adult. Shaba NR: a group of seven fully grown cheetahs, a female and three cubs. Density—interview method: 22 cheetahs; Average of respondents' estimates: 18–21 cheetahs in Samburu and Buffalo Springs (0·060–0·071 cheetah km^{-2}), 11–13 in Shaba (0·046–0·054 cheetah km^{-2}). Cheetahs seen regularly (weekly 75%, monthly 25% of $n = 8$ responses). Trend—stable or increasing population (57% responses, $n = 7$). Possible problem of harassment by tourist vehicles.

Meru National Park
Minimum population—a female and two subadult cubs, a female and one cub, a pair of adults, a four-adult group, an adult male. A lone adult in neighboring Rahole NR. Density—warden in charge estimated 24–30 cheetahs (0·027–0·034 cheetah km^{-2}). Reported weekly to monthly in the park. Trend—stable (100% of $n = 3$ responses).

Lake Bogoria National Reserve
Minimum population—a pair of males and lone individuals seen regularly in reserve and along the lake's shore.

Tsavo National Park
Minimum population—(incomplete record/security conditions). *Tsavo West*: Ngulia and Kilanguni lodge,

next to Mwingio and in the rhino sanctuary (lone cheetahs, one female and three cubs), and Rhino valley–Mzima springs (three adults); south of Tsavo river (a female and six cubs, a single adult), and in Jipe, Ziwani, Losawetho and Serengeti plains. *Tsavo East*: Aruba dam (one female and four cubs), Ndololo–Kanderi swamp (a pair of adults, one adult), Balguda (a pair of adults), and Manyoni (an adult, a group of four including young); Tira plains; Athi river (three adults next to rhino corner), Tsavo Safari Camp (two adults), up river from Tsavo Safari Camp (three groups of four, two, and three). Density–at least 40 individuals (0·002 cheetah km^{-2}). Seemingly most abundant in *Tsavo West* south of the Tsavo River and in *Tsavo East* north of the Galana River. Regularly seen during routine flights over the park (P. Hamilton and D. Woodley, pers. comm.). Neighbouring cheetah locations—Kulalu and Galana ranches East of *Tsavo East*, South Kitui National Reserve, Kiboko Game ranch north of *Tsavo West*, the area of Oloitokitok between Tsavo West and Amboseli National Park, Taita District south of the Voi-Taveta road (Taita Sisal, Taita Hills Game Sanctuary, Luyaneni ranch, Taita ranch, Kasigau ranch).

Taita Hills Game Sanctuary

Minimum population—a female and three mature cubs and a female with two very young offspring seen weekly. An adult male, a group of three (possibly a female and two large cubs) seen irregularly (Reserve's manager, pers. comm.). Density—7–11 (0·062–0·097 cheetah km^{-2}). Trend—increased between 1985 and 1990 (Bundu, pers. comm.).

Nakuru–Naivasha region

Minimum population—Nakuru NP: past records scant (Siemens, 1985). A group of three males regularly seen in 1988 and 1989, occasional sightings of other cheetahs between January and August 1990. Hell's Gate NP: adults seen repeatedly, no cubs. Cheetahs present on Longonot game ranch. All region: at least 20 cheetahs in Nakuru NP, Delamere estate, ADC ranch, Marula estate (Mr Dowson, pers. comm.), and 15 cheetahs in Oserian, Longonot, and Kongoni ranches, and Hell's Gate NP (R. Elliot, pers. comm.). Density—35 cheetahs in region (0·009 cheetah km^{-2}). Trend—Decreasing (67% of $n=6$ responses) on commercial cattle ranches. Threats—isolation from surrounding cheetah populations by proliferation of small scale farms and human settlements to the north and to the west.

Laikipia region

Density—average of respondents' estimates: 76–117 cheetahs (0·015–0·022 cheetah km^{-2}). Trends—50% stable or increasing vs 50% decreasing over last 15 years ($n=24$ responses), extirpated from some small ranches of the plateau periphery (e.g. Suguroi ranch). Threats—important cheetah depredation reported by sheep farmers but not by cattle farmers.