



Aspects of the management of cheetahs, *Acinonyx jubatus jubatus*, trapped on Namibian farmlands

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Abstract

The Namibian cheetah population has recently undergone serious decline due to human-mediated removals, and investigating the rates and causes of such removals is an important aspect of the future management of cheetah populations outside protected areas. We examined cheetahs that were reported live-trapped or killed on Namibian farmlands between 1991 and 1999. A perceived threat to livestock or game led to the vast majority of live captures and to almost half of the cheetah deaths investigated. Despite this, livestock predation from cheetahs appeared to be minimal, and was usually perpetrated by cheetahs with injuries. Most of the cheetahs were trapped in groups, and cheetahs' relative sociality leads to the easy removal of entire social units. Long-term monitoring must include detailed consideration of these indiscriminate removals, as they involve many cheetahs, fluctuate between years, often go unreported, and are likely to have a serious impact on cheetah populations outside protected areas.

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1. Introduction

Intra-guild hostility is emerging as a fundamental element of carnivore communities, with important consequences for distribution and behavior (Hersteinsson and Macdonald 1996). In the case of the cheetah, *Acinonyx jubatus*, it has the practical consequence that their conservation within protected areas is often complicated by conflict with larger predators (Morsbach, 1987; Laurenson, 1995; Nowell and Jackson, 1996; Marker, 1998). Because of such competition in areas with, for example, abundant lions or spotted hyenas, cheetahs are found in greater density on land where these large carnivores have been largely eliminated, as is the case on Namibian farmlands. They therefore occur in areas where they are likely to be in conflict with livestock farmers due both to the development of agriculture and to a reduced wild prey base (Caro, 1994; Marker-Kraus

et al., 1996; Nowell and Jackson, 1996; Marker, 1998). Therefore, whereas the conservation of some large carnivores may lie in protected areas, the survival of the cheetah is also likely to rely upon workable conservation strategies being implemented on farmland.

Most (perhaps 90%) of Namibia's approximately 2500 cheetahs are found in a contiguous 275 000 km² area of commercial livestock and game farmland (Marker-Kraus et al., 1996). There they kill smallstock and cattle calves up to 6 months of age, although the magnitude of their depredations is exaggerated (Marker-Kraus et al., 1996). Cheetahs enjoy protected status in Namibia, but an exemption allows them to be shot in the course of protecting life or property. Despite this protection, Namibian farmers have often removed wild cheetahs as a preventative and largely indiscriminate measure, by either shooting on sight or by live-catching them in traps and placing them in captive situations (Marker-Kraus et al., 1996). The relative sociality of cheetahs enables entire social groups to be removed in one trapping effort, as the calls of one trapped cheetah will attract others in the group into adjoining traps (Marker-Kraus et al., 1996).

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Between 1980 and 1991, the Convention for International Trade for Endangered Species (CITES) reported over 6700 cheetahs 'removed' from the Namibian farmland (CITES, 1992). Considering their protected status, it is startling that during the 1980s Namibian farmers are believed to have halved the cheetah population from 6000 animals to less than 3000 (Morsbach, 1987). This level of culling is clearly a potential threat to the cheetah, and irrespective of ethical considerations, raises the question of whether it is justified economically by reduced stock damage. It is this widespread and indiscriminate capture that is one of the most important factors to understand with relation to managing the cheetah population.

The Cheetah Conservation Fund is a non-profit organization that was established in Namibia in 1991 in an attempt to understand and work towards reducing conflict between farmers and cheetahs on their land. This contact with farmers led to the opportunity to examine cheetahs that were live-trapped or killed on the farmlands and gain information regarding such removals. Interviews with farmers revealed that game farmers had more negative attitudes towards cheetahs on their land than livestock farmers (Marker et al., in press), and we investigated whether this increased level of conflict was reflected in a higher level of cheetah trapping and killing on game farms. When cheetahs were trapped or killed as a result of conflict with livestock farmers, we explored whether there was evidence for actual livestock depredation perpetrated by the removed cheetahs, and whether factors such as age, physical condition or injuries appeared to influence the likelihood of a cheetah causing conflict on a livestock farm. Several studies have found that carnivores causing livestock depredation are disadvantaged in some way, either by an injury, or because they are young animals attempting to hunt alone with little experience (Rabinowitz, 1986; Hoogesteijn et al., 1993; Nowell and Jackson, 1996).

Research conducted on the farmlands revealed that the level of perceived cheetah problems increased significantly through the study period (Marker et al., in press), so we examined whether the rate of cheetah removals also increased through time, whether there were seasonal patterns to removals, and whether the reasons for removing cheetahs changed through time. The conservation and management implications of the resulting information are discussed.

2. Study area

Nearly 6000 commercial livestock farms use 44% of Namibia's available agricultural land (Schneider, 1994; van Schalkwyk, 1995). An estimated 70% of Namibia's huntable game species (Joubert and Mostert, 1975;

Joubert and Morsbach, 1982) are found on these privately owned commercial farms, which includes 90% of the cheetah's habitat and range (Morsbach, 1987).

The study area covers the north-central commercial farmlands, and encompasses the districts of Windhoek, Okahandja, Omaruru, Otjiwarongo, and Grootfontein in the regions of Omahake, Khomas, and Otjozondjupa (between 19°30'S to 23°30'S and 16° E to 19° E). The majority of these commercial farms range in size from 5000 to 20 000 hectares (average 8000 ha) and are primarily bushveld with grasslands suitable for livestock or game. The area is predominately thornbush savanna, consisting of grassland with trees and shrubs in dense or open clumps (Joubert and Mostert, 1975), that is now subject to increasing bush encroachment as a result of livestock overgrazing (Marker-Kraus et al., 1996). The core study area is commercial farmland around the Waterberg Plateau, a 100 km-long elevation that rises 200 m above the surrounding area, which is at approximately 1670 m above sea level.

Namibia has three seasons, as described by Berry (1980), namely a hot dry season from September to December, a hot wet season from January to April and a cold dry season from May to August. Rainfall is highly variable, but mean annual rainfall in the Waterberg study area over a 40-year period was 123.4 mm (± 27.8) for the hot dry season, 348.6 mm (± 58.3) for the hot wet season and 2.8 mm (± 7.4) for the cold dry season.

3. Methods

Between 1991 and 1999, we examined cheetahs that were reported to us after being opportunistically live-trapped or killed on the Namibian farmlands. In order to live-trap cheetahs, farmers used capture cages, usually measuring approximately 2 m \times 0.75 m, with trap release doors at each end and a trigger plate in the middle. Cheetahs were examined either in the field where captured or transported in a 1.2 m \times 0.85 m crate up to 500 km to our research center at Otjiwarongo.

Age classification was based both on personal experience with captive cheetahs and on information from previous studies (Burney, 1980; Caro, 1994) and took into account the weight of the animal, tooth wear and discoloration, gum recession, pelage condition, height, body measurements, the social groupings of animals caught together, and reproductive condition (Marker and Dickman, 2003). Cubs were aged by the proportion of deciduous teeth, extent of adult tooth eruption, and the presence or absence of a mantle (longer, pale fur along the back of the neck and body that is lost at 3 months of age). Using these indicators, cheetahs examined were assigned to one of the following seven age groups:

- (1) Young cubs (6 months old or younger).
- (2) Large cubs (> 6 months to 12 months).
- (3) Adolescents (> 12 months to 18 months).

Cheetahs in these age classes were still considered to be dependent upon their dam.

Independent cheetahs were classified as either:

- (4) Newly independent cheetahs (> 18 months to 30 months).
- (5) Young adults (> 30 months to 48 months).
- (6) Prime adults (> 48 months to 96 months).
- (7) Old/very old adults (> 96 months).

Cheetahs were also classified as to the social group that they were a part of when they were captured or killed. Adult males were either found singly or in coalitions of two to four, while adult females were categorized as either being lone females or females accompanied by dependent cubs. The other social groupings of cheetahs included dependent cubs whose dam was not captured at the same time, and mixed-sex groups of young subadults, which were presumed to be littermate groups. While it was never possible to know without any doubt that all the members of any social group had been captured, the majority of farmers left their traps open for several days after catching a cheetah, and in this way were likely to catch the entire social group. In addition, the ground around a trap was checked for fresh cheetah tracks before a cheetah was taken away, to try to minimize the chances of trapping only part of a social group.

The date, location and reason for capture or killing was recorded, and whether any other individuals were trapped or killed at the same time. Farms were categorized as being either livestock farms, if they were operated using livestock as the primary source of revenue, or game farms, if game provided the major source of income. Some farms did not fit into either category, for instance the Cheetah Conservation Fund farms, which are kept primarily as research areas, and these were categorized as 'other'. In cases where the cheetahs were captured because the farmer perceived them to be a threat to his livestock, evidence was sought regarding whether the cheetahs captured had actually been causing a problem or not. Factors indicating that the cats caught were indeed 'problem animals' included capture on a livestock kill, and capture in or attempting to enter an enclosed livestock kraal near human habitation.

All the cheetahs were given a physical examination, both to gain morphometric and biomedical data, and to examine them for any debilitating attributes such as eye injuries and cataracts, serious injuries to legs and feet, infected wounds, very poor body condition, broken canine teeth and severe mouth injuries. Cases were

excluded where the animal was still a dependent cub, had been held captive for over 30 days, or there was uncertainty regarding whether an injury had been sustained in the wild or while in captivity. During the examination, all cheetahs were marked with both an external ear-tag, as well as a unique internal transponder that was inserted subcutaneously in case the ear-tag was torn out.

Fates of animals after examination included release back into the wild at location of capture, release within 100 km of the capture location, relocation within the country (defined as release further than 100 km from the capture location), translocation out of the country, and being permanently placed in captivity.

Statistical analyses were performed using SPSS version 10.0 software (SPSS Inc. Chicago, USA) and Microsoft Excel 2000 (Microsoft Inc., USA). Means significance testing was carried out using the parametric independent samples *t*-test, while departures from expected ratios were analyzed using a chi-squared test. In addition, the non-parametric Spearman's rank correlation coefficient was used to determine the significance of relationships between variables measured on nominal scales, while Pearson's correlation coefficient was calculated for interval data. All tests were two-tailed unless otherwise stated.

4. Results

Overall, from 1991 to 1999, we performed 376 examinations on cheetahs that had been reported to us after being opportunistically live-trapped on Namibian farmland. Twenty-eight cheetahs were recaptured at least once during the study, including seven that were recaptured twice and two that were recaptured three times, totaling 37 recapture events in all. In addition, 32 necropsies were performed on cheetahs that were killed or found dead in the wild.

Table 1 presents yearly information about capture events, examinations and fates of cheetahs handled. The sex ratio of live captures differed significantly from an expected 1:1 ratio ($\chi^2 = 35.8$, $df = 1$, $P < 0.001$), with a strong bias towards males. The length of time that had elapsed between capture and our examination ranged from 1 to over 100 days, with a mode of 2 days. The majority of cheetahs (57.0%) were examined within 10 days of capture.

4.1. Dates of capture

There was a mean of 40.3 capture events reported annually to CCF between 1991 and 1999, ranging from eight in 1991 to 62 in 1993 (Table 1). There was highly significant variation in the numbers of capture events reported annually ($\chi^2 = 66.3$, $df = 8$, $P < 0.001$). The

Table 1
Breakdown of capture events, necropsies and fates of examined cheetahs through the study period

	Pre 1991		1991		1992		1993			1994			1995			1996			1997			1998			1999			Total			Overall total
	M	F	M	F	M	F	M	F	U	M	F	U	M	F	U	M	F	U	M	F	U	M	F	U	M	F	U				
Original captures	11	2	7	1	19	14	31	21	0	26	9	0	24	11	12	13	0	40	16	33	23	10	10	213	120	0	333				
First examinations	0	0	2	0	17	10	42	22	0	27	14	0	23	10	15	12	0	32	17	40	25	15	10	213	120	0	333				
Necropsies	0	0	0	0	1	0	3	2	1	1	4	2	1	1	3	1	1	0	1	2	1	5	2	16	12	4	32				
Recaptures	0	0	0	0	0	0	10	0	0	5	2	0	9	0	0	0	0	1	0	1	3	4	2	30	7	0	37				
Releases within presumed home range	0	0	0	0	1	1	25	5	0	10	0	0	16	2	3	2	0	4	4	20	11	12	7	91	32	0	123				
Releases outside presumed home range	0	0	0	0	0	0	8	4	0	8	7	0	0	2	4	1	0	8	1	3	3	0	1	31	19	0	50				
Wild into captivity	1	0	2	0	13	8	10	12	0	3	3	0	4	3	1	1	0	22	12	16	10	2	3	74	52	0	126				
Translocations	0	0	0	0	1	0	0	0	0	6	0	0	7	2	4	7	0	0	0	0	0	0	0	18	9	0	27				

number of groups of cheetahs captured each year from 1991 to 1999 also varied significantly ($\chi^2=31.6$, $df=8$, $P<0.001$), ranging from four in 1991 to 32 in 1993, with a mean of 21.7 groups per year from 1991 to 1999. Both the number of individual cheetahs and the number of

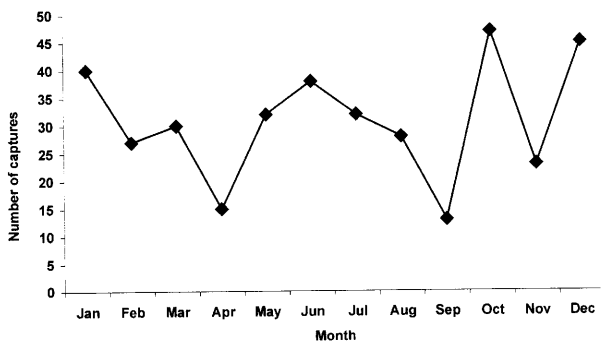


Fig. 1. Month of reported cheetah captures ($n=370$).

social groups reported captured showed a slight increase through the course of the study, although neither trend was significant (individuals: $r=0.47$, $n=10$, $P=0.169$; groups: $r=0.51$, $n=10$, $P=0.137$).

Month of capture was known for 370 of the 376 capture events (Fig. 1). There was a significant variation in the number of cheetahs reported captured by month ($\chi^2=40.7$, $df=11$, $P<0.001$), ranging from 13 to 47 with a mean of 30.8. The main peaks for captures were October, December–January and June.

4.2. Reasons for live capture

The reasons for capture for all 376 live-trapped cheetahs are presented in Fig. 2. The vast majority of cheetahs, 91.2% ($n=343$), were trapped due to farmers perceiving them as a threat to either game or livestock (Table 2). Livestock farmers comprised the significant

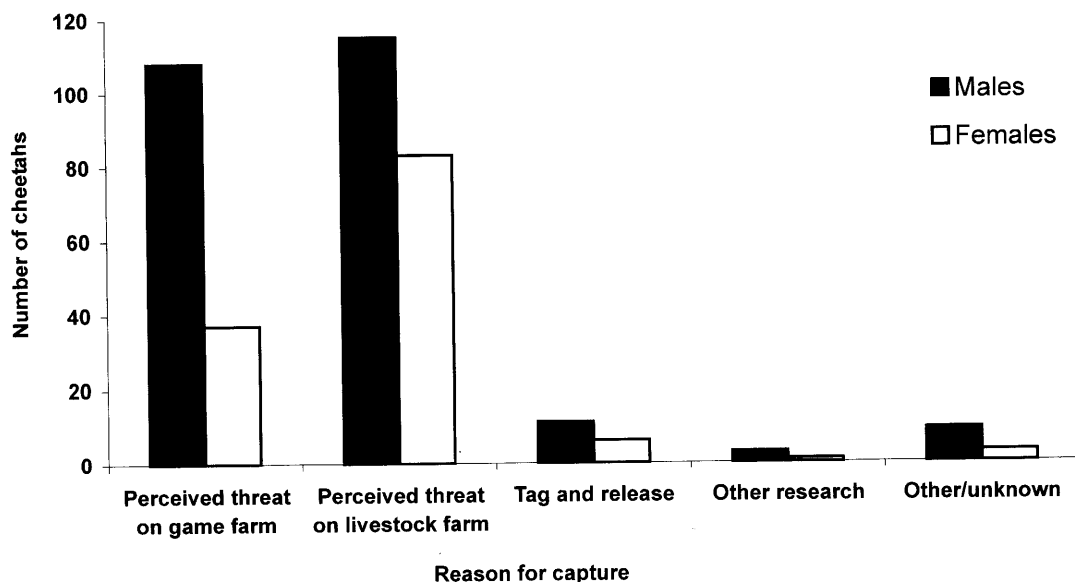


Fig. 2. Reasons for all live cheetah captures reported throughout the study ($n=376$).

Table 2
Demographics of cheetahs examined, broken down by reason for capture

Reason for capture	Single males	Total no. males	Total no. coalition	Mean coalition size	Single females		Total no. cubs with mother		Total no. cubs without mother		Total no. litters		Total no. litters group size	Total no. animals	Total no. groups			
					Females with cubs	Females without cubs	Total no. cubs with mother		Total no. cubs without mother		Total no. litters							
							M	F	Total	M	F	Total				M	F	Total
Threat on game farm	31	21	50	2.4	12	7	16	6	22	8	10	18	13	3	2	5	145	86
Threat on livestock farm	22	15	35	2.3	13	17	25	25	50	28	21	49	24	5	7	12	198	96
Other	11	3	6	2.0	5	2	3	3	6	3	0	3	1	0	0	0	33	22
Total	64	36	85	2.2	30	26	44	34	78	39	31	70	38	14	9	23	376	204

Table 3
Breakdown of social structure and group sizes captured on different farm types

Social group	No. captured on game farms	No. expected on game farms	No. captured on livestock farms	No. expected on livestock farms	Test statistic (A)	df	P	Mean group size on game farm	Mean group size on livestock farm	Test statistic (B)	df	P
Single males	31	25.1	22	27.9	2.65	1	0.103	–	–	–	–	–
Male coalitions	50	40.2	35	44.8	4.53	1	0.033*	2.4	2.3	0.217	34	0.829
Single females	12	11.8	13	13.2	0.01	1	0.944	–	–	–	–	–
Females with cubs	7	11.4	17	12.6	3.17	1	0.075	3.1	2.8	0.699	22	0.492
Unaccompanied cubs	18	31.7	49	35.3	11.22	1	0.001**	1.4	2	-2.06	35	0.047*
Littermate groups	5	8	12	9	2.18	1	0.140	2.5	2.4	0.205	5	0.846

(A) = Chi-squared test. (B) = Independent samples t-test.
* Significant at the $P < 0.05$ level. ** Significant at the $P < 0.01$ level.

majority of the 91 farmers that reported trapping cheetahs for this reason ($\chi^2=22.3$, $df=1$, $P=0.001$), and significantly more cheetahs (57.7%) were reported captured in response to a perceived threat to livestock than to game ($\chi^2=8.2$, $df=1$, $P=0.004$). However, the ratio of farm types on which captures were conducted to reduce threats was 74.7% livestock farms to 25.3% game farms. Using these as expected ratios for captures, it became evident that disproportionately more cheetahs were in fact captured on game farms as a threat than on livestock farms ($\chi^2=51.8$, $df=1$, $P<0.001$). This did not appear to be an effect of different farm sizes: size was known for 71 of the 91 farms reporting captures, and there was no significant difference in size between game and livestock farms ($t=0.83$, $df=69$, $P=0.410$).

When captures performed to reduce threats were examined by social group, 96 (52.7%) social groups were trapped on livestock farms, while 86 (47.3%) groups were captured on game farms (Table 2). Using these as expected ratios, significantly more coalition males were trapped as a perceived threat on game farms, while significantly more unaccompanied cubs were captured on livestock farms (Table 3). When group sizes were examined between the different farm types, the group size of cubs trapped without a dam was greater on livestock farms, accounting for the higher number of unaccompanied cubs captured on livestock farms. There were no statistically significant differences for any of the other social groups. The percentage of cheetahs examined that were reported captured due to a perceived threat to game or livestock decreased significantly through the course of the study ($r=-0.88$, $n=10$, $P=0.001$).

4.3. Age and sex structure of captured cheetahs

Cheetahs captured for different reasons varied significantly in terms of age group at capture (KW $\chi^2=23.9$, $df=4$, $P<0.001$; Fig. 3). When cheetahs captured as threats to either livestock or game were examined, disproportionately more young cubs and large cubs were trapped on livestock farms than game farms, although the figure for large cubs only touched statistical significance (young cubs: $\chi^2=9.06$, $df=1$, $P=0.003$; large cubs: $\chi^2=3.89$, $df=1$, $P=0.049$). Conversely, young adults and prime adults were captured significantly more often as a threat on game farms than livestock farms (young adults: $\chi^2=8.91$, $df=1$, $P=0.003$; prime adults: $\chi^2=3.99$, $df=1$, $P=0.046$).

Forty-two percent ($n=83$) of the cheetahs captured as a threat on game farms were female, compared to only 26% ($n=37$) of those captured as a threat on livestock farms and 35% ($n=120$) for the overall sample population. There was therefore a significant relationship between sex and farm type, for those cheetahs trapped as a threat to livestock or game ($\chi^2=9.90$, $df=1$, $P=0.002$).

4.4. Physical condition

Overall, 11.4% ($n=43$) of the cheetahs examined had a serious physical impediment that had the potential to reduce their hunting ability (Table 4). There was no significant difference in the frequency of potential problems between the overall sample population and those trapped as being threats ($\chi^2=0.001$, $df=1$, $P=0.986$), nor any significant difference observed between cheetahs captured as a perceived threat on game farms and those

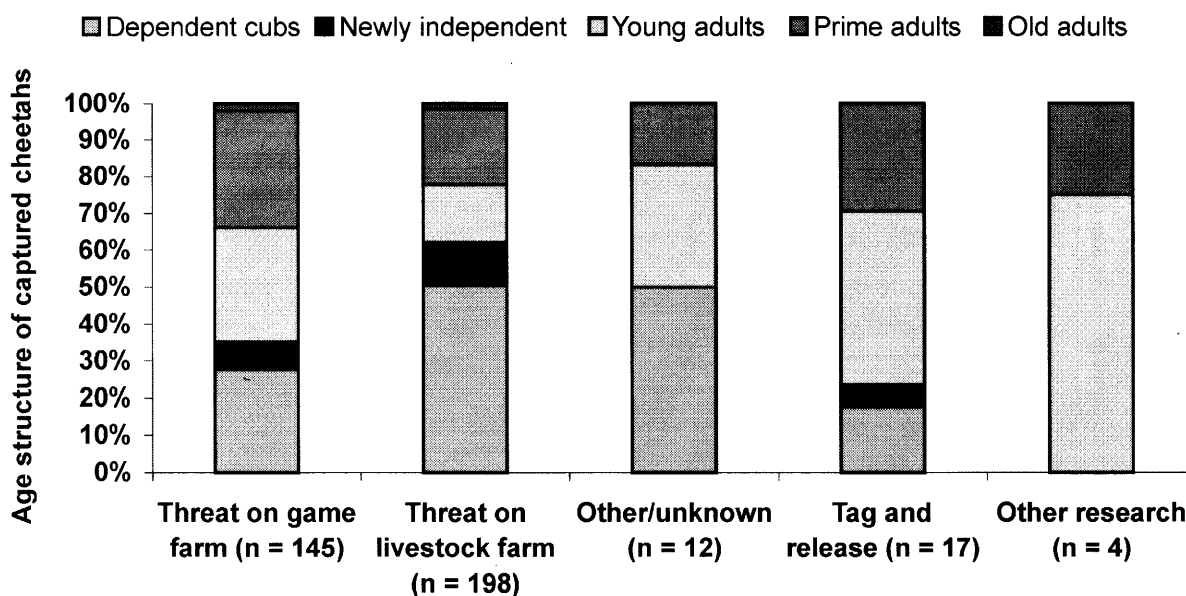


Fig. 3. Age structure of cheetahs reported captured for different reasons ($n=376$).

Table 4
Incidence of physical problems, examined by reason for capture and by social group

	Overall sample population (<i>n</i> = 376)	All adults examined (<i>n</i> = 227)	Adults trapped as threat on game or livestock farm (<i>n</i> = 203)	Adults trapped as threat on game farm (<i>n</i> = 105)	Adults trapped as threat on livestock farm (<i>n</i> = 98)	Cheetahs probably taking livestock (<i>n</i> = 6)	Single males (<i>n</i> = 64)	Coalition males (<i>n</i> = 91)	Single females (<i>n</i> = 30)	Females with cubs (<i>n</i> = 26)	Cubs trapped without dam (<i>n</i> = 70)	Littermates (<i>n</i> = 78)
% Healthy cheetahs	88.6	85.9	86.2	85.7	86.7	33.3	89.1	84.6	82.8	84.6	91.4	93.6
% Cheetahs with a physical problem	11.4	14.1	13.8	14.3	13.3	66.7	10.9	15.4	17.2	15.4	8.6	6.4
Chi-squared statistic	–	1.64	1.15	0.87	0.34	18.1	0.14	1.43	0.98	0.41	0.55	1.92
df	–	1	1	1	1	1	1	1	1	1	1	1
<i>P</i>	–	0.201	0.283	0.352	0.561	<0.000**	0.907	0.232	0.322	0.523	0.456	0.166

** Significant at *P* < 0.001 level.

on livestock farms ($\chi^2 = 0.31$, *df* = 1, *P* = 0.860). When examined by social group, there were no significant deviations from the frequency of problems seen in the overall population for any group (Table 4).

Although 198 cheetahs were captured through the study due to a perceived threat to livestock, there were only six cases (3.0%) where there was at least circumstantial evidence that the cheetah captured was indeed taking livestock. Of these six cats, four had serious physical problems that could hinder their normal hunting technique. One had a badly injured paw, another had a very swollen foot and evidence of a respiratory problem, with harsh breathing and mucus coming from his nose, a third was in very poor condition and emaciated, and the fourth had a badly swollen foot and a broken upper canine. There was therefore a significant relationship between the occurrence of physical problems and the likelihood of preying upon livestock ($\chi^2 = 19.6$, *df* = 1, *P* < 0.001), with cheetahs apparently taking livestock showing a much higher frequency of problems than the overall sample population. There was no evident relationship between whether or not a cheetah was likely to be causing problems when it was trapped and either age ($z = -1.74$, *P* = 0.082) or sex ($\chi^2 = 0.01$, *df* = 1, *P* = 0.932).

4.5. Fates after capture

Not all the captured cheetahs were removed, as some farmers were willing to have the cheetahs that they captured marked and then released back onto their land. To gain a better understanding of the level of removal on different farm types, we examined the eventual fates of captured cheetahs.

Of the 369 live cheetahs handled for which fates were recorded, 45.8% (*n* = 169) were held in captivity following examination, including 43 that were in permanent captivity prior to the examination and 126 wild cheetahs that were subsequently placed in captivity. Nearly half of the wild cheetahs entering captivity (47%) were cubs captured on their own and were too young (i.e. aged < 18 months old) for release without a dam, while refusals by game and livestock farmers to allow releases accounted for 45% of captive placements (Fig. 4).

Of the 145 cheetahs that were trapped on game farms as a perceived threat, 115 were potentially releasable (i.e. healthy animals of independent age, or cubs that could have been released with their dam). Of these, 29.6% (*n* = 34) were placed in permanent captivity due to the farmer's refusal to allow a release. Similarly, refusal by livestock farmers to release accounted for the captive placement of 30.0% (*n* = 36) of the 120 cats caught for posing a threat to livestock that had potential for release. There was therefore no significant difference between game and livestock farmers regarding the percentage of healthy cheetahs that they decided not

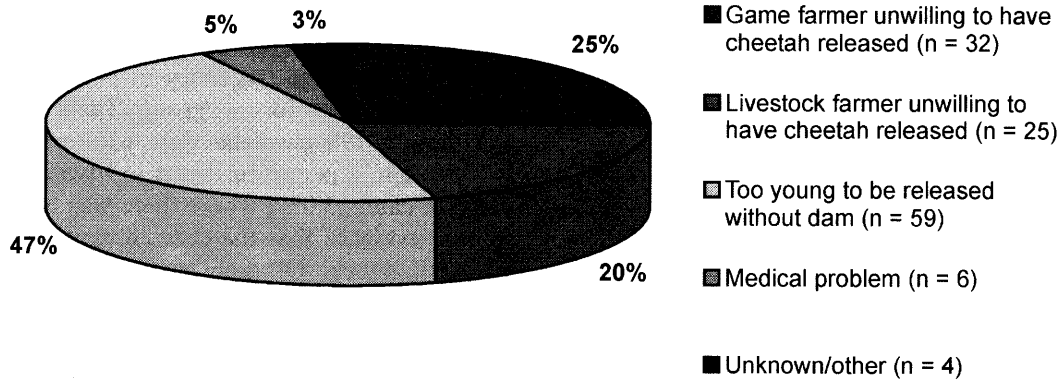


Fig. 4. Reasons for wild cheetahs entering captivity after examination (n = 126).

to release ($\chi^2=0.007$, $df=1$, $P=0.933$). Although both game and livestock farmers showed some decline in the level of refusals through the study (Fig. 5), these trends were not statistically significant (game farmers: $r_s=-0.276$, $n=9$, $P=0.472$; livestock farmers: $r_s=-0.275$, $n=8$, $P=0.509$).

After examination, 46.9% (n = 173) of the 369 cheetahs were released back into the wild in Namibia. The majority of these, 71.1% (n = 123) were released either at site of capture or within their presumed home range, and 28.9% (n = 50) were relocated elsewhere within the country. Relocation distances varied from 100 to 600 km from the site of capture, with a mean of 213 km. Of the remaining cheetahs, 7.3% (n = 27) were translocated out of the country for re-introduction in other countries; 24 went to South Africa and three to Zambia.

The sex of captured cheetahs did not appear to be an important factor in terms of eventual fate—the sex ratio of wild cheetahs that entered captivity did not differ significantly from that of the overall capture population ($\chi^2=2.48$, $df=1$, $P=0.116$). Similarly, the sex ratio of cheetahs that farmers refused to release did not differ significantly from the sex ratio of releasable animals, either on game farms ($\chi^2=1.20$, $df=1$, $P=0.274$) or livestock farms ($\chi^2=0.88$, $df=1$, $P=0.348$), and there

was no relationship between sex and whether cheetahs were released within or outside their home range ($z=-1.55$, $P=0.121$).

4.6. Causes of death

During the study period 63 (40 males, 20 females and three of unknown sex) deaths of wild cheetahs were recorded. As with captures, the sex ratio of the reported deaths was significantly biased towards males ($\chi^2=6.67$, $df=1$, $P=0.010$). Human-caused mortality accounted for 79.4% (n = 50) of the deaths of wild cheetahs examined (Fig. 6). Ten were accidental deaths, including five in the wild and five in capture cages, while the remain-

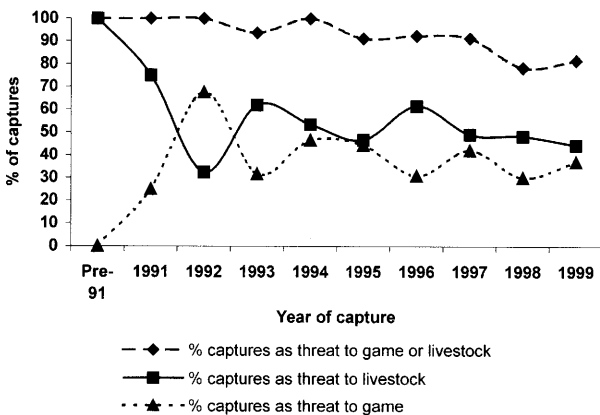


Fig. 5. Trends in the percentage of captures reportedly conducted to protect livestock or game throughout the study.

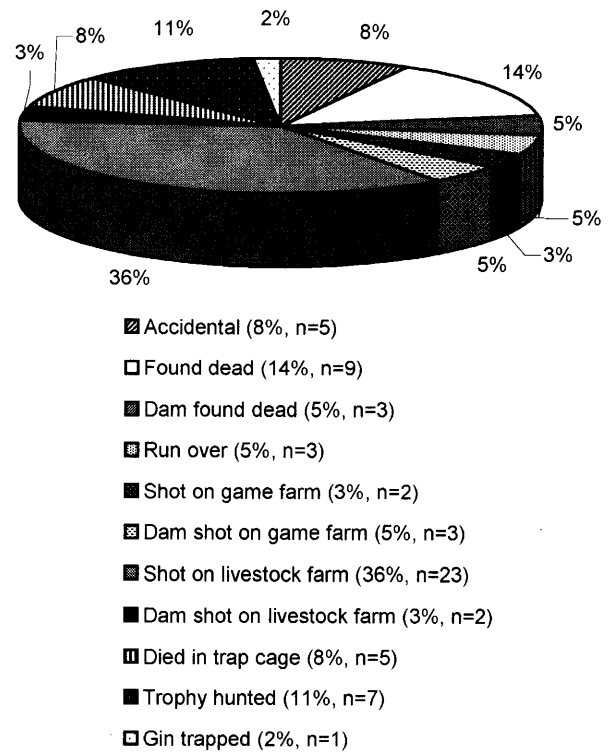


Fig. 6. Reported causes of death for wild cheetahs through the study (n = 63).

ing 40 were deliberate killings, including five males and two females that were trophy hunted. Although more of these deliberate killings occurred on livestock farms ($n=25$) than on game farms ($n=15$), the difference was not significant ($\chi^2=2.50$, $df=1$, $P=0.114$).

The main cause of deliberate killings, accounting for 25 cheetahs, was being shot due to being a perceived threat, of which 92.0% were shot on livestock farms and 8.0% on game farms. In addition to these direct deaths from shooting, three cubs were assumed to have died after their dam was shot on a game farm, and two cubs were assumed to have died when their dam was shot on a livestock farm. Overall, therefore, shooting as a protective measure accounted for 47.6% ($n=30$) of the total reported mortality in the wild. Trophy hunting, by comparison, accounted for only 11% of overall reported deaths.

4.7. Overall removals

Combining the data on human-caused mortality with that regarding wild cheetahs entering captivity and those translocated allows an overview of the number of cheetahs reported to the Cheetah Conservation Fund as removed from the Namibian farmlands each year. In total, 203 of the examined cheetahs (123 males, 78 females and two of unknown sex) were removed during the study period, including 126 captive placements, 50 human-caused deaths and 27 translocations. Most ($n=118$, 58.1%) of these removals were directly attributable to the attitudes of game and livestock farmers. There was no significant difference between game and livestock farmers regarding the overall number of removals ($\chi^2=0.31$, $df=1$, $P=0.501$).

5. Discussion

Determining the rates and causes of removal from a population are vital to understanding the threats to its continued viability and how best it can be managed with regard to long-term, sustainable utilization. Understanding the causative factors that lead to removals allows future management plans to be focused on the important areas of conflict between humans and cheetahs and to identify possible solutions.

These issues are particularly important with regard to the Namibian cheetah population, the vast majority of which occurs on privately owned land rather than in reserves, leading to a large potential for conflict, and which underwent a dramatic decline in the past (CITES, 1992). The indiscriminate removal of cheetahs, which is unstable and fluctuates annually, must be understood both when considering quotas for legal utilization such as trophy hunting, and for formulating management plans. We have presented data regarding all cheetah

captures reported to us throughout the study, but it is difficult to know the proportion of captures that went unreported, and how representative these data are in terms of the scenario nationwide. Nevertheless, any detailed information regarding reasons for cheetah removal is very important, and can help guide future conservation efforts so that suitable strategies can be implemented that will not threaten the long-term survival of the population.

The significant variation in the number of captures reported each year shows that indiscriminate removals are likely to fluctuate highly between years, making management of removals and an understanding of their long-term effects more difficult. There was no indication that the number of cheetahs trapped or removed annually had declined through the study period. However, it is difficult to interpret whether a change in the level of reported removals in a given year is a true effect or rather a result of variation in the reporting rate of such removals. The reported reasons for capture did change through time, however, with the proportion of captures conducted to protect livestock or game, rather than for tag-and-release or research purposes, declining significantly through the study.

There was significant seasonal variation in the level of captures, and the peaks seen in October, December–January and June are important as these times correspond with the main calving seasons in Namibia (Marker-Kraus et al., 1996). Farmers tend to increase their trapping effort around these times as a preventative measure against livestock loss. However, introducing management techniques such as synchronizing calving seasons within and between farms and using calving corrals and guarding animals has been shown to be more effective in reducing losses than indiscriminately removing predators (Marker-Kraus et al., 1996).

During the study, the motivation for trapping 91.2% of cheetahs examined was a perceived threat to livestock or game. Previous studies have shown that actual loss of livestock to cheetahs is far less than is commonly thought (Marker-Kraus et al., 1996). This study supported that, as only 3% of the cheetahs trapped as a perceived threat to livestock were actually likely to have been causing livestock loss. Additionally, predation of game by cheetahs is natural behavior; therefore, cheetahs captured in game farms should not on these criteria be perceived as ‘problem’ animals. However, the continued perception of cheetahs as a significant threat to livestock and game is clearly of vital importance with regard to reducing indiscriminate removal and must be addressed. As discussed earlier, the use of correct livestock management measures are more effective at reducing stock losses than indiscriminate predator removals (Marker-Kraus et al., 1996). Effective game farm management techniques include the exclusion of predators through proper maintenance (e.g. electrification) of

perimeter fencing, the stocking of native game species, which are less susceptible to predation than exotic species (Marker-Kraus et al., 1996), and the formation of conservancies, which has been effective in reducing farmer–predator conflicts and in improving game management (Marker-Kraus et al., 1996). Previous research has been influential in the formation of new wildlife laws that promote the development of conservancies (Marker and Schumann, 1998), and legislate that game farms cannot be managed in a way that is detrimental to wildlife.

Cheetahs causing livestock losses, but that are suitable for relocation back into the wild, should be considered for relocation to re-establish or supplement populations in protected areas such as national parks where domestic livestock does not occur. This could have an important impact in increasing genetic diversity within existing cheetah populations, as cheetahs have exceptionally low heterozygosity (O'Brien et al., 1983), which could potentially cause problems as populations become further isolated and fragmented. Cheetahs not suitable for re-release should be made available to supply the need for new bloodlines in captivity, taking the pressure off non-problem wild cheetahs. Such movements within Namibia should be monitored through an official body such as the Large Carnivore Management Association.

The trend seen that slightly more females with cubs were trapped on livestock rather than game farms could be taken to indicate that they were more likely to resort to stock-taking due to the pressures of raising a litter. It is possible, however, that farmers increase their trapping effort upon seeing the signs of a female with cubs not in response to greater stock loss but rather as a preventative measure.

However, removing cheetahs indiscriminately, particularly if the farmer is not experiencing current problems, may actually create problems rather than preventing them, for example, by creating a 'vacuum' through the removal of dominant adults from an area. The resulting available range is likely to become occupied by younger, inexperienced dispersing animals, which may resort to taking livestock as easier prey (Marker-Kraus et al., 1996).

The unusually high frequency of problems amongst cheetahs likely to be causing livestock loss, compared with the general adult population, indicates that these problems may be causative in making cheetahs prey upon domestic stock, rather than it being usual hunting behavior, as is commonly thought by farmers. Although adult males are more prone to intra-specific aggression and there is a greater likelihood of them sustaining injuries during fights over dominance, mates or territory-holding, there was no significant variation in the incidence of physical problems between different social groups.

After examination, 34% of previously wild cheetahs entered captivity, mainly due to the capture of cheetahs that were too young to be released alone. The capture of young cheetahs without a dam means that those animals are unable to be released back into the wild, and could be made available for captive breeding programs to legitimate national or international zoological facilities to maintain their genetic lines. Live export of cheetahs is permitted by the CITES quota, but during 2000 Namibia stopped all export of cheetahs to zoological facilities, in an attempt to reduce market demand and stop indiscriminate catching (M.E.T., 2000).

Farmer attitudes accounted for almost all the remaining wild cheetahs that entered captivity, and there were no significant differences in the reported level of removals between game or livestock farmers. Although the perception of cheetahs posing a significant threat to livestock is a long-standing one, in many cases it is exaggerated in relation to the actual number of cheetahs that cause losses. The predation upon game is a more difficult problem, as it is clearly natural behavior, and in many cases game can only be protected through the exclusion of predators such as cheetahs. Nearly half of the cheetahs examined were released back into the wild; the majority (71.1%) back into their own home range. Initial analysis from a companion study at the Cheetah Conservation Fund has shown that relocation of cheetahs is a viable option in cases where the farmers are unwilling to have them released nearby (L. Marker, unpublished data). Further analysis of data gathered through radio-tracking these cheetahs will reveal the tendency to move back towards their original capture site, which is a common concern amongst farmers allowing relocation.

It is important to realize, though, that most of the releases reported here occurred as a direct result of long-term contact and work with farmers on a relatively small percentage of Namibia's farmlands. For the rest of the country, further from the core study area, releases are probably less likely and the number of trapped cheetahs alone may give the best indication of the level of removal on farms nationwide.

The translocations that occurred during this study were important in the successful re-establishment of the cheetah population in the Hluhluwe-Umfolozi Park, which took place over a two year period of time. In addition, the translocations helped to establish a cheetah population in Phinda, and were experimental in Zambia. These translocations stopped in 1996 after farmers began to allow more tag and release or radio-collaring of cheetahs within Namibia. Despite having been removed from the Namibian population, these translocations have played an important role in developing schemes for the cooperative management of cheetahs between different range states. In the future, such cooperative management will become an increasingly

important component of cheetah conservation, and has been identified as a component of a Global Cheetah Masterplan (Grisham, 2000).

The most common reported cause of death in the wild was shooting by livestock farmers, accounting for over a third of all deaths, and human-caused mortality appeared to outweigh natural causes of death, although there is some inherent bias towards human mortality by relying on deaths reported by people. The number of removals, both live-trapping and deaths, in this study show that the Namibian cheetah population still undergoes a substantial offtake on an annual basis, especially as previous research shows that these numbers are likely to be only a small fraction of the actual total removals (Marker-Kraus et al., 1996).

Of the cheetahs that underwent necropsies, only seven were trophy hunted animals. The limited number of cheetahs trophy hunted can be of only minimal consequence to the population, especially when compared with the large numbers of cheetahs killed indiscriminately. However, the utilization of female cheetahs should be limited (Berry et al., 1996), and they are not recommended as trophy animals (NAPHA, 1995; M.E.T., 1999).

6. Implications for cheetah conservation

Cheetahs actively seek to avoid larger predators such as lions and spotted hyenas, instead dispersing into areas with low densities of these competitors (Durant, 1998). The Namibian farmlands provide an excellent refuge from larger carnivores but provoke a conflict instead with the farmers who consider them a threat to their livestock and game. This results in widespread trapping, often performed as a preventative measure rather than in response to an actual problem, and leads to the removal of many cheetahs on an annual basis.

The most important step towards reducing such removals is continued extension work with farmers on livestock and game management techniques to decrease losses to predators and diminish the perception of cheetahs as pests. The same issues are relevant in other range countries, and are being addressed through collaborations between farmers and conservationists, for example, the National Cheetah Management Program in South Africa and the Cheetah Working Group in Zimbabwe. In addition, well-regulated trophy hunting and community-based ecotourism are both viable options for giving cheetahs increased economic value on the farmlands and providing an incentive to reduce indiscriminate removals.

Where the removal of cheetahs is unavoidable, relocation is a viable alternative to killing them, as is the translocation into suitable areas with a viable prey base in other countries to supplement their cheetah popula-

tions. These movements involve complex issues, however, and must be done with thorough planning and adequate monitoring to be effective. If release is not possible, then moving the cheetah into a recognized national or international captive breeding facility should be an option in order to maintain genetic diversity and provide educational and conservation benefits. Meanwhile, continued monitoring of removals from the Namibian cheetah population will provide additional data, which can be used alongside those presented here in formulating future management plans and population models for effective conservation efforts.

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