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Demography of the Namibian cheetah, *Acinonyx jubatus jubatus*

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Abstract

Namibian cheetahs have suffered, and continue to suffer, high levels of removal due to conflict with local farmers, and it is important to understand the demography of this population in order to determine its likely persistence. Examination of cheetahs reported live-trapped or killed by local farmers, combined with subsequent information from radio-telemetry, allowed demographic parameters such as sex ratios, age and social structure, litter size, interbirth intervals and survivorship to be estimated for cheetahs on Namibian farmlands. Cub mortality was relatively low, but adult mortality was high, particularly for males, and peaked at 5–6 years of age. Neither marking nor relocating cheetahs seemed to affect survivorship, and there was no difference in survivorship between the sexes. Time spent in captivity did not appear to affect survival after release. These findings will be useful in formulating recommendations regarding the conservation and sustainable utilization of cheetah populations outside protected areas.

Keywords: Demography; Survival; Mortality; Reproductive parameters; Cheetahs; *Acinonyx jubatus*; Namibia

1. Introduction

Determining vital rates and demographic parameters is fundamentally important to the accurate understanding of any population (Eberhardt, 1985; Lebreton et al., 1992; Lebreton et al., 1993). When a population is subject to high offtake, it is essential to establish whether the level of removal threatens its long-term viability. Large mammals are particularly sensitive in light of their long gestation and interbirth intervals, extended parental care and long maturation. Their life history parameters effectively lower the potential rate of population increase (Eisenberg, 1981; Harvey et al., 1989), creating a higher extinction risk. Adult survival is a particularly important parameter, documented to exert a substantial impact on population viability for large, long-lived species (Eberhardt, 1985; Taylor et al., 1987; Doak et al., 1994; Crooks et al., 1998).

The Namibian cheetah, *Acinonyx jubatus jubatus*, is a threatened population which has been subject to a high level of removal, and whose vital rates require more accurate determination in order to assess and manage the impact of such removals. Vital rates of cheetahs have been reported in the Serengeti (Caro, 1994; Laurenson, 1995; Laurenson et al., 1995; Kelly et al., 1998; Kelly and Durant, 2000), but the population in Namibia is subject to strikingly different pressures (Marker-Kraus et al., 1996). In Namibia, around 90% of cheetahs are found not in protected areas but on commercial farmlands, where competition with other large carnivores is minimal but which brings them into direct conflict with farmers (Marker-Kraus et al., 1996). As a result of this conflict, an estimated 7000 cheetahs were removed from the Namibian population between 1980 and 1991 (CITES, 1992), with an average of 827 cheetahs removed annually between 1978 and 1985, and 297 per year between 1986 and 1995 (Nowell, 1996). The average number of cheetah removals reported to Namibia's Ministry of Environment and Tourism between 1998 and 2000 was 118 per year. The majority of cheetah mortality reported to the Cheetah Conservation Fund involves adults, which, if representative of the country-wide situation, could have severe impacts in terms of long-term population viability (Crooks et al., 1998).

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In order to ascertain the impact of such mortality, this paper reports and examines the vital rates and life history parameters of cheetahs on Namibian farmlands. Assessment of these reproduction and survivorship estimates provides insight into the vulnerability and likely persistence of the cheetah population in Namibia. In 1996, a Population and Habitat Viability Assessment was conducted, and called for, as a priority, more data on demographic parameters such as annual female mortality and reproductive information (Berry et al., 1996). Here, we provide these data.

2. Methods

2.1. *Study area*

The study area covers 2 672 000 hectares of the commercial farmlands of north-central Namibia, representing 7.3% of the total Namibian farmlands and 14.5% of the commercial cattle farmlands. The area 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 the 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. Most farming practices are mixed with cattle and some small-stock (goats and sheep) living alongside free-ranging wildlife species. The region is predominately thornbush savanna, consisting of grassland with trees and shrubs in dense or open clumps (Joubert and Mostert, 1975).

The core study area is farmland around the Waterberg Plateau, a 100 km-long elevation that rises 1870 m above sea level. Farms at around 1670 m above sea level surround the plateau, and these constitute the principal study sites.

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. Annual rainfall is highly variable, with the majority of rain falling between November and April. The mean annual rainfall in the Waterberg study area over a 40-year period was 123.4mm (±27.8) for the hot dry season, 348.6mm (±58.3) for the hot wet season and 2.8mm (±7.4) for the cold dry season.

2.2. *Trapping, immobilizing and marking cheetahs*

Demographic parameters were estimated using data from cheetahs captured opportunistically by farmers between 1991 and 2000. Some of these cheetahs were subsequently radio-collared and released, which provided information regarding reproduction and survivorship in the wild. Our interpretations take note of a potential bias in the sample population arising from the high proportion of cheetahs captured at specific trees used as scent-marking posts, which are used predominantly by adult males (Marker-Kraus and Kraus, 1995).

The cages used for live-trapping cheetahs typically measured 2 m × 0.75 m, with trap release doors at each end and a trigger plate in the middle. Cheetahs were examined either at the capture site or were transported in a squeeze/transport crate (1.2 m × 0.85 m) to the Cheetah Conservation Fund's center near Otjiwarongo. Immobilization was achieved in the capture cage or squeeze/transport crate by using a hand syringe or blowpipe, while cheetahs in a holding compound were darted using an air-pump dart gun (Telinject, Germany) or blowpipe (Telinject, Germany). In all immobilizing procedures, the anesthetic agent (Telazol: Tiletamine HCI and Zolazepam HCI, Fort Dodge, Iowa, USA) was administered intramuscularly in the hindquarters at a concentration of 100 mg/ml with a normal dose of 4 mg/kg. The animals showed signs of sedation within 4–6 min and were recumbent within 8–10 min.

Each cheetah was marked with a uniquely numbered concerted transponder (Trovan Electronic Identification Systems, model-ID 100) placed at the base of its tail, and/or an aluminum ear-tag with a unique ID number in the individual's ear. On designated animals (those released in the core study area), a neoprene radio-telemetry collar with external antenna was also fitted (Advanced Telemetry Systems, Minnesota). The radio-collars were 3.8 cm wide with an adjustable strap from 30 to 45 cm long, with a 30-cm antenna extending about 18 cm from the collar. The collars were fitted with a "C" cell lithium battery with a life expectancy of over 36 months. Radio-collars weighed 280 g and were equivalent to 0.56% of body mass for a 50 kg male and 0.76% for a 37 kg female, well below the limit suggested by Amlaner and Macdonald (1980). In line with Laurenson and Caro (1994), we could detect no impact of these collars on cheetah survival.

2.3. *Age classification*

Age classification was based both on 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, body measurements, the social groupings of animals caught together, and reproductive condition. The cheetahs examined were assigned to one of the following eight age groups using these indicators:

(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 adults (>96 to 144 months).
(8) Very old adults (over 144 months).

It was also possible to age cheetahs more accurately within these age groups by using information gained by examining teeth and other factors such as presence or absence of a mantle (longer, pale fur along the back of the neck and body that starts to diminish at 3 months of age). In cheetahs, deciduous teeth erupt at 28–30 days old, and by 45–50 days all the molars have erupted. Leg spots and the yellow coat coloring develop at 6–7 weeks old, and the loss of the mantle starts at 3–4 months. The lower incisors are lost at 7 months old, while adult teeth start to come in at around 8 months. By 9.5 months old, the last adult molars have erupted. Cheetahs between 6 and 12 months old still have long fur on the back of the neck, although it is no longer a defined mantle. They acquire two-thirds of adult size at 12 months old, but do not reach adult weight until around 24 months old.

In mature animals, the degree of tartar and yellowing on the teeth, wear of canine tips, muscle mass, recession of gums, signs of wear on pads, scarring, and body measurements can all be used to estimate age within the set groups, as being at the beginning, the middle or the older end of the age category. An estimation of actual age was marked down alongside the age group, and was felt to be accurate due to the substantial experience of one of the authors (L.M.) with the examination of both captive animals of known age and repeated examinations of re-caught wild animals, also of known age. Additionally, lower premolar teeth from dead cheetahs are now being used for cementum ageing (Matson's Laboratory, LLC, Milltown, MT, USA), and this technique is providing comparative information for estimating ages in this study, with preliminary results showing a good correlation between estimated and actual ages.

2.4. Determining social structure

Cheetahs are relatively social felids and often occur in groups: in many cases, farmers left adjoining traps open after catching a cheetah, to ensure that all members of any social group were captured at the same time. In other instances, capture was more random and it was likely that other cheetahs in the same social group remained free. Parameters such as coalition size, litter size and age-specific cub mortality were therefore determined using data from cases where determined attempts had been made to capture the entire group of cheetahs. Cheetahs were classified as to the social group of which they were a part when they were captured, using the following categories. Males over 18 months old were classed either as single males or as members of male coalitions, while females over 18 months old were classed as either being single females or as mothers trapped with cubs. The remaining classes were cubs (18 months old or younger) trapped without a dam, and mixed-sex groups of young independent cheetahs (19–24 months old), which were presumed to be littermate groups.

2.5. Estimating reproductive parameters

Age at parturition was estimated by examining females trapped with cubs, and by observing new litters of cubs produced by radio-collared females of known age. Long-term monitoring of six radio-collared females that had multiple litters provided information regarding interbirth intervals. Information regarding the distribution of births through the year was gathered from the examination and ageing of cubs trapped, and from observations made of females and cubs during radio-telemetry.

Litter size was determined from groups trapped where concerted efforts had been made to capture the entire family unit, and from observations of radio-collared females with cubs during aerial tracking. Although we have no data regarding litter size at birth, observations of litters of different ages gave some indication of age-specific cub mortality.

2.6. Estimating mortality and survivorship

Most cheetahs were released at site of capture, but when this was not possible, the cheetahs were relocated. Relocation was classified as being 100 km or more away, as this should be well beyond a normal home range: average home range for male cheetahs is 1122 km^2 and for females is 1591 km^2, with diameters of 18.9 and 22.5 km, respectively (Marker, 2000).

The majority of cheetahs released within the core study area were radio-collared in order to gain information regarding post-release movements and home ranges. In addition, the tracking of cheetahs enabled information to be gathered regarding survivorship. Wild cheetah deaths reported to CCF included cheetahs that had been radio-collared, some that were tagged, and some that had not been marked at all. The deaths of marked cheetahs, whether radio-collared or simply ear-tagged, were often reported and enabled comparisons to be made about the approximate age of death of handled cheetahs versus those of cheetahs that had never been handled.

Mortality rates and life expectancy data were calculated following Downing (1980). The age of a cheetah at death was taken to be the midpoint of the age category in which it was recorded at the time of death. By using this midpoint, the formulae used should underestimate and overestimate the age at death for equal numbers of cheetahs and thereby give an approximation that is close to the actual distribution of ages at death.

2.7. *Data analysis*

Statistical analyses were performed using SPSS version 10.0 software (SPSS Inc. Chicago, USA). Means significance testing was carried out using the parametric independent samples *t*-test, using Levene's test to determine equality of variances, while departures from expected ratios were analyzed using a chi-squared test. 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 determined for interval data. Other tests performed included one-way analysis of variance, and log rank for the equality of survival distributions following a Kaplan Meier analysis. All tests were two-tailed unless otherwise stated.

3. Results

3.1. *Social structure*

The 412 cheetahs examined through the study were captured in 228 social groups, as summarized in Table 1. One-hundred and seventy adult males were reported trapped, of which at least 97 (51.2%) were in coalitions. Coalition size ranged from 2 to 4, with a mean of 2.3 throughout the study ($n=42$). The majority of coalitions (76.2%, $n=32$) were comprised of two males, while 16.7% ($n=7$) had three members and 7.1% ($n=3$) had four, although these data should be interpreted with some caution, as despite all efforts, some coalition members may have avoided capture. Mean coalition size showed no significant change through the course of the study ($F=1.11$, df $=10$, $P=0.389$), but the percentage of adult males trapped in coalitions did decline significantly over time ($r_s=-0.833$, $n=10$, $P=0.003$; Fig. 1).

3.2. *Age and sex structure of sample population*

A summary of the age structure of captured cheetahs through the study is shown in Fig. 2. There was a highly significant variation in overall capture frequency for each age cohort ($F=2.02$, df $=10$, $P=0.030$). Assuming that captures reflect trends in the wild population, the

Table 1
Annual demographic breakdown of the sample population into social groupings throughout the study period

Year	Single males	Total no. coalitions	Total no. coalition males	Mean coalition size	Single females	Females with cubs	Total no. cubs with mother			Mean litter size with mother	Total no. cubs without mother			Total no. litters without mother	Mean litter size without mother	Total no. littermates			Total no. litters	Mean littermate group size	Total no. animals	Total no. groups
							M	F	Total		M	F	Total			M	F	Total				
Pre-1991	5	2	4	2.0	0	0	0	0	0	–	1	1	2	1	2.0	1	1	2	1	2.0	13	9
1991	1	2	6	3.0	0	0	0	0	0	-	0	1	1	1	1.0	0	0	0	0		8	4
1992	2	3	8	2.7	6	3	5	2	7	2.3	3	3	6	4	1.5	1	1	2	1	2.0	34	19
1993	10	8	18	2.3	2	4	6	6	12	3.0	4	3	7	4	1.8	4	6	10	4	2.5	63	32
1994	8	6	16	2.7	4	2	2	2	4	2.0	4	2	6	4	1.5	2	1	3	1	3.0	43	25
1995	8	8	17	2.1	3	3	6	3	9	3.0	2	3	5	2	2.5	0	0	0	0	–	45	24
1996	1	2	4	2.0	3	2	4	5	9	4.5	4	3	7	4	1.8	0	0	0	0	–	26	12
1997	11	3	8	2.7	2	3	8	3	11	3.7	14	8	22	12	1.8	0	0	0	0		57	31
1998	9	4	8	2.0	3	7	11	9	20	2.9	6	7	13	7	1.9	0	0	0	0	–	60	30
1999	9	1	2	2.0	7	2	2	4	6	3.0	1	0	1	1	1.0	0	0	0	0	–	27	20
2000	9	3	6	2.0	3	1	2	1	3	3.0	4	5	9	4	2.3	2	3	5	2	2.5	36	22
Total	73	42	97	2.3	33	27	46	35	81	3.0	43	36	79	44	1.7	10	12	22	9	2.4	412	228

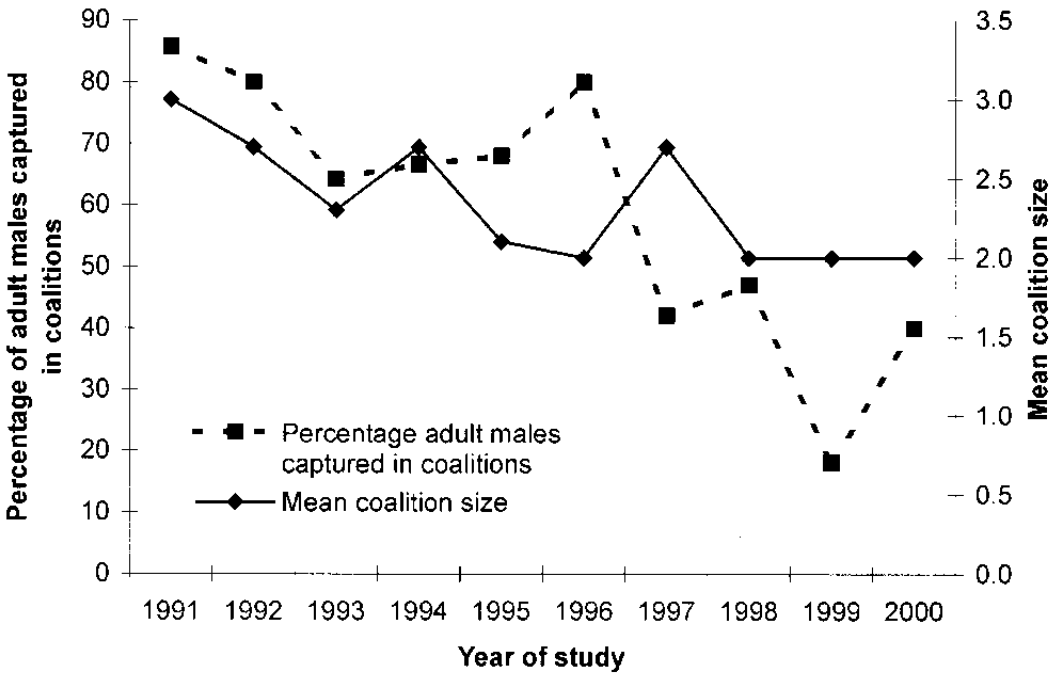

Fig. 1. Proportion of adult males captured in coalitions throughout the study period 1991–1999, and mean coalition size (*n*=42 coalitions).

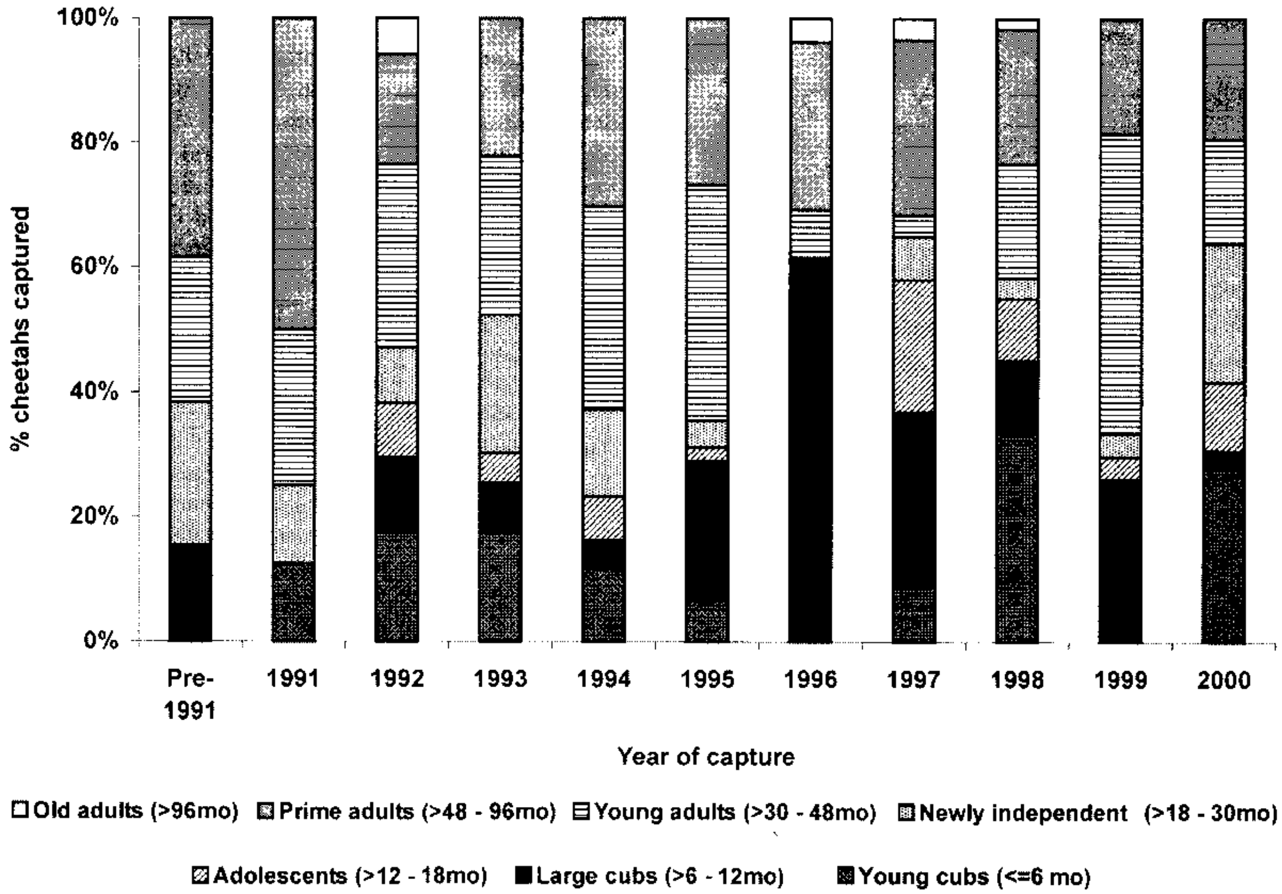

Fig. 2. Classification of sample population of captured cheetahs by year into seven age categories.

age structure of the population was not stable, with young animals making up a greater proportion of captured animals as the study progressed ($r_s = -0.12$, $n = 412$, $P = 0.016$), and the percentage of dependent cubs (aged ≤18 months) captured significantly increasing through time ($r = -0.833$, $n = 11$, $P = 0.003$; Fig. 3).

There was a strong bias towards capturing adult males, with 2.9 adult males captured for every adult female. This proved to be a significant deviation from a 1:1 sex ratio with regard to the adult cheetahs trapped ($\chi^2 = 47.1$, df = 1, $P < 0.001$).

3.3. Reproductive parameters

The majority of litters studied ($n = 43$) were produced by females of prime age, but successful breeding was also recorded for young adults and old animals (Fig. 4). The percentage of adult females that were trapped with cubs each year ranged from 22.2% to 70.0%, with an overall mean of 44.5% ($n = 60$), but showed no significant trend over time ($r_s = -0.23$, $n = 9$, $P = 0.557$).

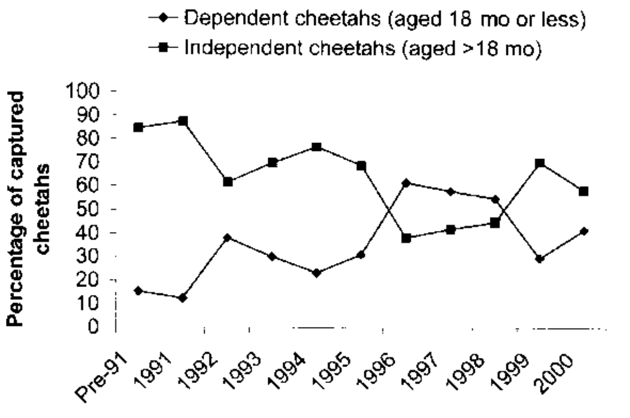

Fig. 3. Percentages of dependent (≤18 months old) and independent cheetahs (> 18 months old) in the sample population of cheetahs captured through the study.

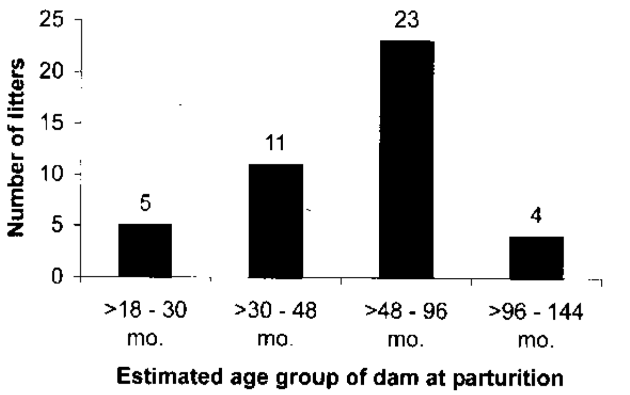

Fig. 4. Estimated age group of dam at birth of litter, using data gathered from both live capture and radio-tracking ($n = 43$ litters).

Litters were produced throughout the year, but the number recorded born varied between months ($\chi^2 = 18.3$, $n = 10$, $P = 0.05$), indicating some degree of seasonality. Birth peaks were evident in March and June–July, with 40% of litters born in these months, while only 5% of litters were born from October to December (Fig. 5).

Litter size obtained through trapping ranged from 1 to 6 with a mode of 3 (mean = 3.1, $n = 27$ litters), with no statistically significant variation between years ($F = 0.56$, df = 26, $P = 0.812$). Litters observed during radio-telemetry alone ranged in size from 2 to 5 with equal modes of 3 and 4 cubs (mean = 3.4, $n = 13$ litters), and also did not vary significantly between years ($F = 2.51$, df = 12, $P = 0.131$). There was no significant difference in mean litter size observed between the two techniques ($t = -0.93$, df = 38, $P = 0.357$). Overall, therefore, the mean litter size observed, using data gathered from both methods, was 3.2 post-emergence ($n = 40$ litters, Fig. 6). This does not provide information regarding litter size at birth, however, and there is likely to be pre-emergence mortality in the den (Laurenson et al., 1992). There was no significant deviation from an expected 1:1 sex ratio regarding cubs aged 12 months old or below ($\chi^2 = 0.62$, df = 1, $P = 0.432$). Repeated observations of litters of different ages provided some information regarding age-specific cub mortality prior to independence (Fig. 7).

While females were captured with as many as six dependent cubs, average litter size for newly independent littermates ranged from one to three with a mode of 2 and a mean of 2.4 ($n = 9$ litters). This may be an underestimate, however, if newly independent animals are less likely to stay with a trapped littermate and are therefore less likely to be captured and recorded.

Reproductive information was gathered on 19 litters from 10 radio-collared dams (Table 2). Interbirth intervals following litters that were raised to independence ($n = 6$) ranged from 21 to 28 months, with a mean of 24 months.

Although cheetahs have been known to survive for up to 21 years in captivity (Marker-Kraus, 1997) the maximum age recorded here for an animal that was still reproductively active was 12 years, so this can be regarded as the figure for effective longevity.

3.4. Mortality and survivorship

Mortality rates were calculated from all recorded wild deaths ($n = 67$), including 45 marked cheetahs and 22 that had never been handled (Table 3). These data show that the age specific mortality ranged from 20% to 28% for the first 3 years of life and then dropped to virtually zero between three and five. There was then a large peak of mortality at age 5–6, but of the few cheetahs that reached 6 years of age ($n = 4$), all survived for a further 4 years.

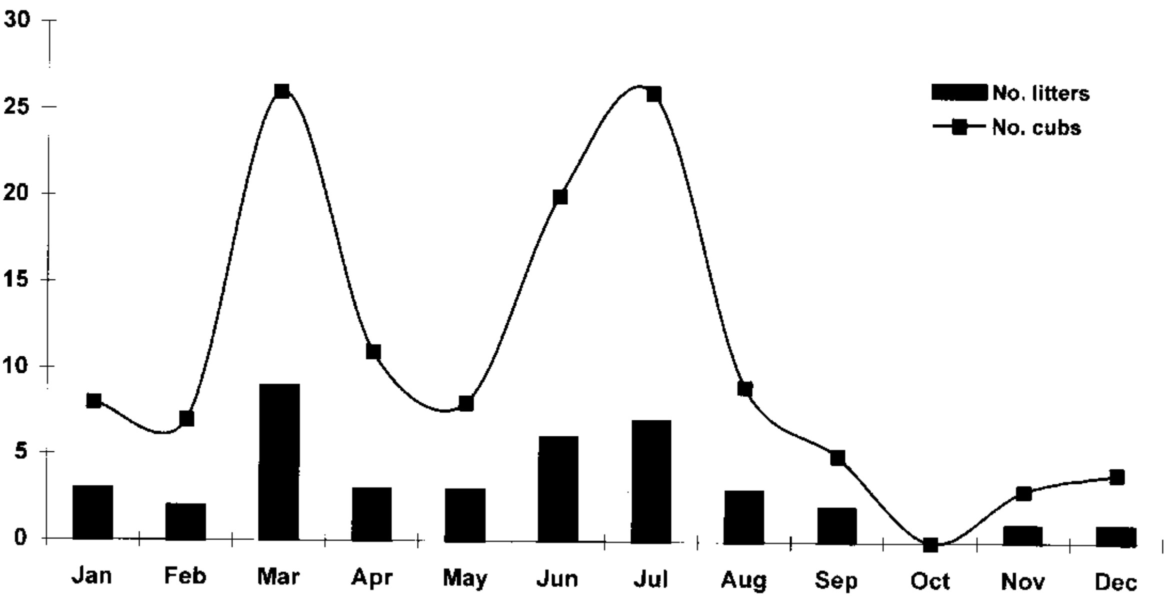

Fig. 5. Estimated month of birth for all litters of cubs handled during the study period ($n = 40$ litters, containing 127 cubs).

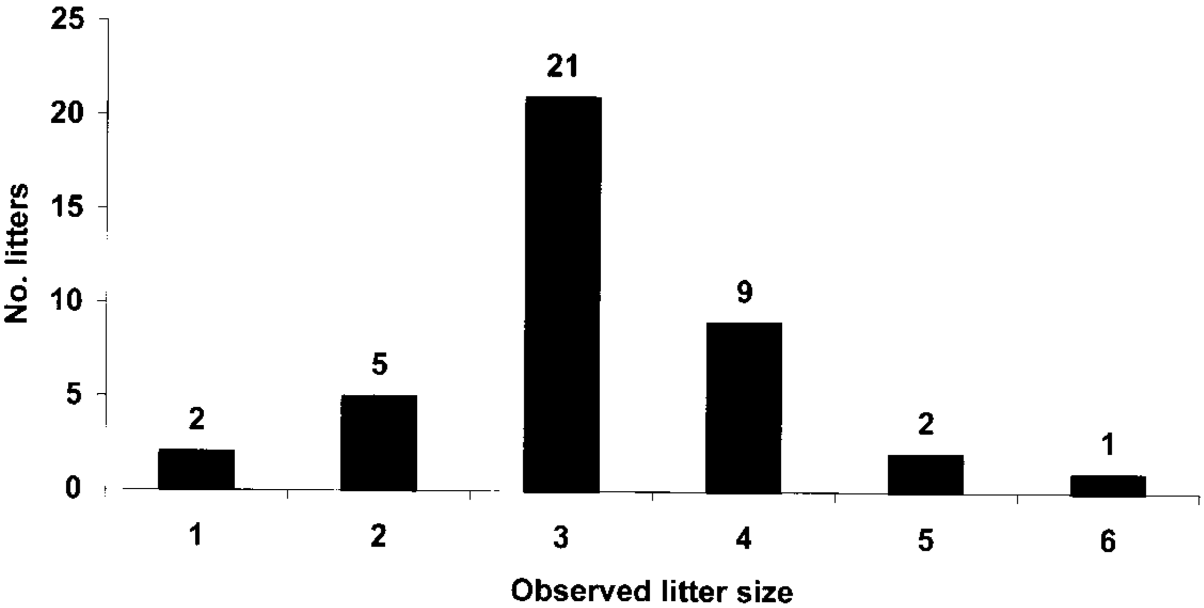

Fig. 6. Litter sizes observed through both live capture and radio-tracking throughout the study period ($n = 40$ litters).

Survivorship following release could be calculated for the 45 wild marked cheetahs, and ranged from 0.6 months to 48.5 months for males ($n = 35$) and 0.6 months to 65.4 months for females ($n = 10$). Survivorship of male and female marked cheetahs is shown in Fig. 8. Of these cheetahs, 71.1% ($n = 32$) were adults at the time of release, of which 46.9% ($n = 15$) were of prime breeding age. Mean survival time for tagged and released males was 14.4 months ($n = 35$), while for females it was 18.5 months ($n = 10$). Although females lived for slightly longer, the difference in survivorship was not statistically significant (log rank = 0.71, df = 1, $P = 0.401$). When analysis was restricted to adult animals, to remove any effect of cub mortality following the death of a female, the mean survival time was 16.2 months for males ($n = 23$) and 20.3 months for females ($n = 9$), a difference that again was not significant (log rank = 0.58, df = 1, $P = 0.447$). There was no significant difference in estimated age at release between the sexes ($t = 0.24$, df = 30, $P = 0.812$).

Cumulative annual survival was calculated for both sexes of radio-collared cheetahs (Fig. 9 a and b). There was a significant difference between cumulative yearly survival rates between males (mean = 9.4 months) and females (mean = 10.2 months) ($t = 2.07$, df = 22, $P = 0.009$). There was also a significant difference

Table 3
Life table showing mortality rates for wild cheetahs throughout the study period

Age (years)	q_x			$l_{\times 100}$			$d_{\times 100}$			L_x			e_x		
	M	F	Overall	M	F	Overall	M	F	Overall	M	F	Overall	M	F	Overall
0–1	0.22	0.29	0.25	100	100	100	22.22	29.41	24.53	88.89	85.29	87.74	3.53	3.21	3.42
1–2	0.18	0.25	0.20	77.78	70.59	75.47	13.89	17.65	15.09	70.83	61.76	67.92	3.39	3.33	3.38
2–3	0.30	0.22	0.28	63.89	52.94	60.38	19.44	11.76	16.98	54.17	47.06	51.89	3.02	3.28	3.09
3–4	0.06	0.00	0.04	44.44	41.18	43.40	2.78	0.00	1.89	43.06	41.18	42.45	3.13	3.07	3.11
4–5	0.00	0.00	0.00	41.67	41.18	41.51	0.00	0.00	0.00	41.67	41.18	41.51	2.30	2.07	2.23
5–6	0.80	0.86	0.82	41.67	41.18	41.51	33.33	35.29	33.96	25.00	23.53	24.53	1.30	1.07	1.23
6–7	0.00	0.00	0.00	8.33	5.88	7.55	0.00	0.00	0.00	8.33	5.88	7.55	3.50	3.50	3.50
7–8	0.00	0.00	0.00	8.33	5.88	7.55	0.00	0.00	0.00	8.33	5.88	7.55	2.50	2.50	2.50
8–9	0.00	0.00	0.00	8.33	5.88	7.55	0.00	0.00	0.00	8.33	5.88	7.55	1.50	1.50	1.50
9–10	1.00	1.00	1.00	8.33	5.88	7.55	8.33	5.88	7.55	4.17	2.94	3.77	0.50	0.50	0.50

q_x = age specific mortality rate. $l_{\times 100}$ = number attaining this age from a beginning cohort of 100. $d_{\times 100}$ = number dying at each age from a beginning cohort of 100. L_x = mean number alive between age classes. e_x = mean expectation of life (average additional lifespan of those reaching this age).

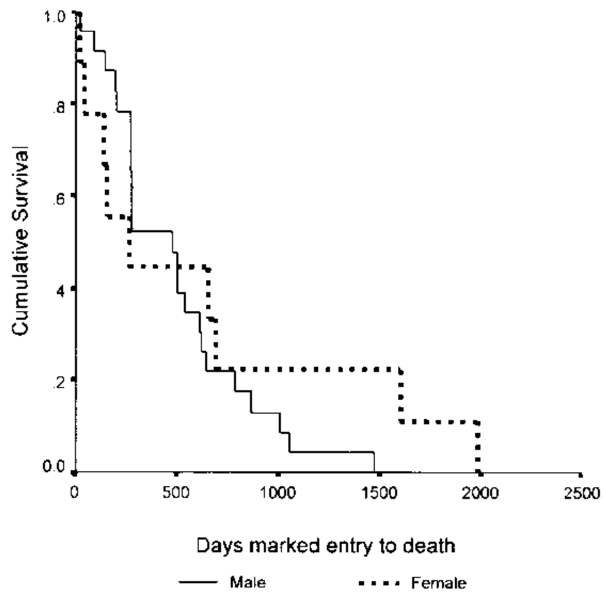

Fig. 8. Post-release survivorship of marked adult male cheetahs ($n=35$) compared with marked adult female cheetahs ($n=10$).

radio-collared cheetahs was 20.2 months ($n=24$), whereas cheetahs wearing only a tag survived on average for 9.8 months after release ($n=8$): see Fig. 10. Radio-collared cheetahs survived longer following release than tagged cats, and differed significantly in their survival distribution (log rank = 3.92, df = 1, $P=0.048$). This was not an effect of differing ages at release between the two groups ($t=-1.23$, df = 30, $P=0.230$).

It is possible that since all cheetahs radio-collared were in our core research area, more people were aware of the presence of marked cheetahs which was a deterrent to killing cheetahs, whereas ear-tagging of cheetahs took place throughout the country, including places where many people were unaware of our research. There were 21 reported cases of human-caused mortality amongst the marked animals, and if the radio-collar acted as a deterrent then the expectation would be for there to be relatively few collared cheetahs within this sample. In fact, 14 of the 21 cheetahs reported killed by humans were radio-collared, which was not a significant deviation from an equal ratio of collared to tagged cats. However, 36.8% of the released adult cheetahs were radio-collared, while 63.2% were only tagged. Using these proportions as the expected ratios, radio-collared cheetahs comprise a significantly greater percentage of human-caused mortality than would be expected ($\chi^2=8.05$, df = 1, $P=0.005$).

Often cheetahs with health problems spent longer time in captivity before release than healthy cheetahs. To investigate whether time spent in captivity was detrimental in terms of subsequent survival in the wild, survivorship following release for adult animals was correlated with total days spent captive prior to release, which ranged from zero (release on day of capture) to 389, with a mean of 38 days ($n=131$). There was no statistically significant relationship between the two variables ($r=-0.52$, $n=32$, $P=0.778$).

Cheetahs were either released at site of capture or distances varying between 50 and 600 km away from the capture location. There was no significant difference in mean survivorship for adult cheetahs released at the site of capture (mean = 18.0 months, $n=19$, $s=13.6$), those released within 100 km of the capture site (mean = 15.4 months, $n=7$, $s=9.1$) and those relocated over 100 km away (mean = 28.4 months, $n=8$, $s=27.3$) ($F=1.34$, df = 2, $P=0.275$).

4. Discussion

4.1. Social structure

The most common age groups trapped were young adults and prime adults; population growth rates for large, long-lived mammals are likely to be especially

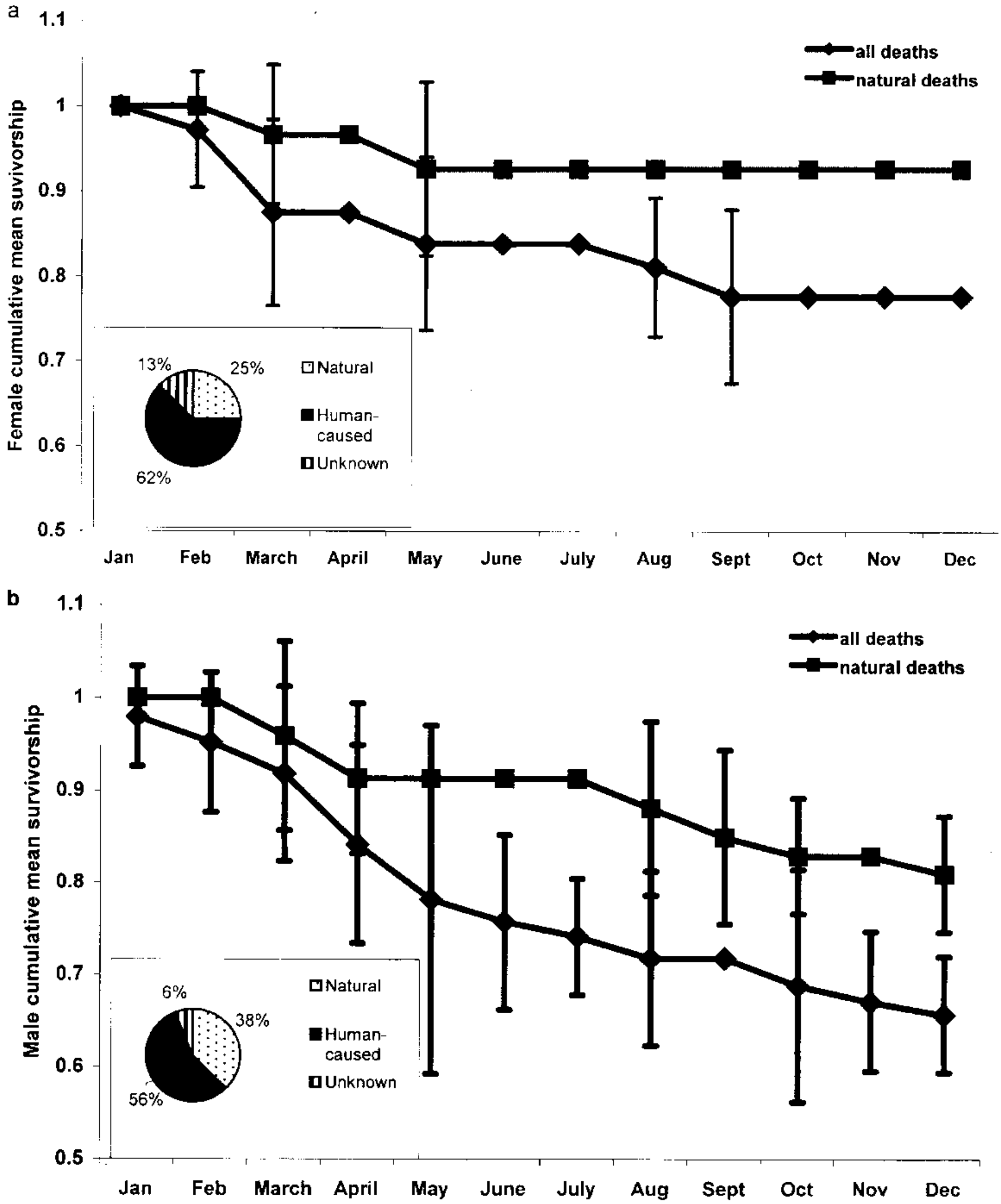

Fig. 9. Annual cumulative survivorship for (a) adult female and (b) adult male cheetahs, showing the breakdown into natural and human-caused mortality. Error bars represent standard errors.

sensitive to adult mortality, so removal of these age classes is likely to have a particularly detrimental effect on the population (Crooks et al., 1998). If this sample is representative of the nationwide picture, then this finding is of particular concern. Males are often caught at the time of dispersal when they are trying to establish a territory, traveling long distances across many farms, presumably increasing their chances of being trapped. This bias towards young adult and prime adult males is likely to be a sampling bias rather than a true indication of population structure in the wild, due to the aforementioned bias due to capture at scent-marking posts.

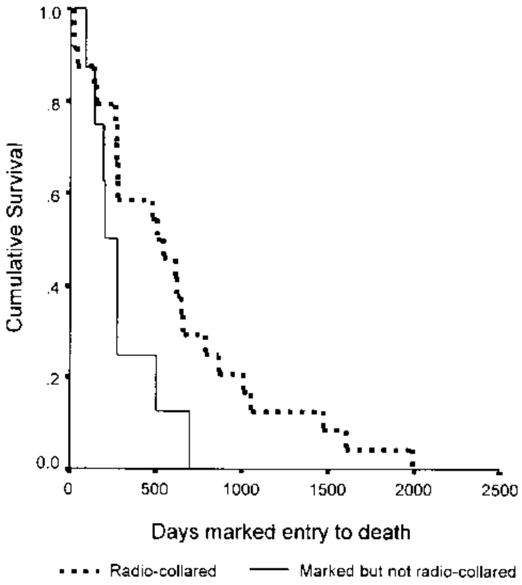

Fig. 10. Post-release survivorship of adult cheetahs that were radio-collared ($n=24$) compared with those that were handled and marked but not radio-collared ($n=8$).

The disproportionate removal of males has been seen in many mammalian species, and the wide-ranging behavior exhibited by cheetahs mean that a relatively high degree of male removal would by itself have comparatively little impact on the population as a whole. However, although these male removals are probably less damaging to the viability of the population than a skew towards removing females, they can nevertheless have serious impacts in terms of social structure and behavior (Tuyttens and Macdonald, 2000). In areas of fragmented populations and low density where removed males cannot easily be replaced by immigrants, continued removal of adult males could have a severe effect and lead to lower reproductive rates and an accelerated decline (Tuyttens and Macdonald, 2000). This scenario is likely to become of greater importance if cheetah populations become more fragmented in the future. The removal of dominant, territorial males can also be counter-productive to farmers insofar as it may lead to the increased survival of subadult and transient animals that would not normally settle in the area (Young and Ruff, 1982, cited in Tuyttens and Macdonald (2000) and which may be more likely to become 'problem' animals (Marker-Kraus et al., 1996).

4.2. Reproductive parameters

The live capture of females with cubs presented the opportunity to monitor the sex structure of cubs and to estimate reproductive parameters. Litters could not be studied before emergence from the den, and therefore provide no direct information regarding either sex structure or litter size at birth, as infant mortality can be substantial before emergence (Laurenson, 1994). The litter size at emergence of 3.2 found in this study was slightly less than the 3.6 reported from the Serengeti (Caro, 1994), but litter size at independence was slightly higher (2.4 compared with 2.1 in the Serengeti; Kelly et al., 1998). Although females are capable of breeding at an earlier age (Wildt et al., 1993; Marker-Kraus, 1997), reproduction on the Namibian farmlands usually does not occur before 2.5–3 years of age (Morsbach, 1987). Similarly, whereas males are physiologically capable of breeding at less than 2 years of age (Wildt et al., 1993; Marker-Kraus, 1997), social constraints may limit breeding of Namibian male cheetahs to older, territorial animals in the prime age category.

4.3. Mortality and survivorship

The mortality and life expectancy data reveal that for both male and female cheetahs in our sampled population, the highest peak of deaths is between 5 and 6 years of age. This is to be expected given that the trapping and removal methods tend to select prime breeding age adults, as discussed earlier. The mortality figure found here for the first year of life (25%) should be interpreted with caution as it cannot include mortality before emergence from the den, which has been found to be a period of high mortality in other studies (Laurenson, 1994). However, it appears that in Namibia, the level of cub mortality is indeed far lower than in game reserves with a high density of intra-guild competitors. Despite this, even without intra-guild competition, fewer than 50% of the cubs reach independence. Data from the Serengeti show that female cheetahs surviving to independence had a good chance of reaching old age (Kelly et al., 1998). This was not the case here: in this study, female cheetahs that reached independence still had an 86% chance of dying before 6 years of age. This reflects the differing pressures on the two populations: in the Serengeti, the greatest threat to survival is predation by larger carnivores, particularly lions, on dependent cubs (Laurenson, 1994). This threat recedes once a cheetah reaches adulthood, whereas the greatest threat to cheetahs in Namibia appears to be human-caused and focuses on cheetahs of prime breeding age. In this study the threshold seemed to be 6 years of age; the few cheetahs monitored that lived that long managed to survive until old age.

The removal of adult cheetahs has been shown to have a far more significant impact on the overall population than the removal of cubs (Crooks et al., 1998). The selection by trapping adult cheetahs is therefore of major concern regarding the ability of the Namibian cheetah population to persist long-term. The majority of these removals are in reaction to a perceived threat to livestock and/or game by commercial farmers (Marker-Kraus et al., 1996). As a result, conservation efforts should be concentrated on educating farmers in alternative game and livestock management techniques to reduce losses and lessen conflict.

Much of the information gathered through this study was only possible by directly handling cheetahs, including fitting radio-collars prior to release. However, the invasive handling and monitoring of wildlife, particularly when it involves an endangered species, has been the focus of much debate (Driscoll and Bateson, 1986; Bateson, 1991; Cuthill, 1991; Smith and Boyd, 1991; Burrows et al., 1994; Creel et al., 1997). The handling of wild animals is likely to involve some degree of stress (Laurenson and Caro, 1994), and it has been argued that this may hamper the eventual survival of the animals (Martin and Bateson, 1986; Cuthill, 1991), perhaps by compromising the immune response and increasing the risk of disease outbreaks (Burrows et al., 1994). This may be particularly important with cheetahs, whose inherent genetic uniformity may make them more vulnerable to the impact of disease (O'Brien et al., 1985; Smith and Boyd, 1991; Laurenson and Caro, 1994; Terio, 2000). However, this study showed that the survivorship of wild cheetahs we handled and marked was no lower than that of wild cheetahs that had never been handled. In addition, there was no evidence that putting a radio-collar on a wild cheetah had a negative impact on survival following release, and the radio-collared cheetahs studied here lived longer post-release than their tagged counterparts. Collaring of cheetahs was conducted in a relatively concentrated area, where farmers were well aware of the research being conducted. Therefore, public awareness may have contributed to the longevity of radio-collared cheetahs that are not causing problems with farmers. Marking of cheetahs in other parts of the country, where public awareness was not as extensive, may have caused the differences between the post-release longevity. It could not be ascertained whether the collars acted as a deterrent to farmers who would otherwise kill the cats, instead prompting them to contact CCF or another authority to deal with problem or trapped cheetahs. The higher than expected incidence of radio-collared cheetahs amongst those killed by humans may indicate that people are more likely to report a death if they see a radio-collar on the cheetah concerned.

Cheetahs that were relocated far from their capture site provided important survival information. The relocated cheetahs did not have significantly different survival rates from those released in close proximity to their capture site, which suggests that relocating cheetahs into suitable habitat can be an effective conservation strategy without negatively impacting the survivorship of the individual cheetah.

Of importance in our monitoring was the possible effect of keeping cheetahs in captivity prior to release. There is a chance that holding an animal in captivity could have a detrimental effect on survivorship after release, either through a reduction in physical fitness and hunting ability, or by animals losing their territories and being forced into marginal areas. Analysis of cheetahs we handled, however, showed that there was no relationship between the length of time spent in captivity and subsequent survivorship following release, despite the fact that some of the cheetahs were held in captivity due to being in poorer physical condition.

From this 10-year study we have identified certain areas of concern, for example, the continued removal of prime adults from the population, the skewed sex ratio resulting from capture methodology and the apparently unstable age distribution. In addition, we have been able to establish parameters that can be used in future modeling efforts. Such modeling exercises will provide a basis for long-term conservation strategies for cheetahs on Namibian farmlands.

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