Quantifying prey preferences of free-ranging Namibian cheetahs

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The cheetah (*Acinonyx jubatus*) has long been regarded as a significant threat to the interests of farmers of both game and livestock in Namibia and for this reason has been removed in large numbers. However, the diet of these cheetahs has not been documented; such documentation is an important component of any effective conservation plan. We performed feeding trials to relate more accurately the remains found in cheetah scats to the number of prey animals consumed. Using scat analysis techniques, we found that cheetah prey size ranged from birds and hares to large antelope. They rarely preyed on domestic stock, with apparent selection towards common, indigenous game species. Information gathered from aerial sightings of kills was significantly biased towards larger prey species. Data on the number of times cheetahs were seen near livestock or game were found to not be representative of the type of prey taken when compared to corrected scat analysis. Due to the diurnal nature and wide-ranging habits of cheetahs, they are sighted relatively frequently near stock, which may contribute to an exaggerated perception of their predation on stock. From the results of this study, livestock predation by cheetahs was estimated to account for at least 0.01 calves and 0.004 sheep per km^2 on the Namibian farmlands, and may be substantially more depending on cheetah density. Any stock losses as a result of cheetahs and other predators can have economic impacts for farmers, and management techniques for mitigating such losses are suggested. The use of controlled feeding trials and subsequent calculation of a correction factor for scat analysis could be a valuable tool for gaining a more accurate estimate of carnivore diet in future studies.

Key words: *Acinonyx jubatus,* cheetah, feeding ecology, livestock predation, scat analysis.

INTRODUCTION

The cheetah, *Acinonyx jubatus,* is Africa's most endangered large felid, with the largest remaining free-ranging population of around 2500 individuals existing in Namibia (Morsbach 1987; Marker-Kraus & Kraus 1995; Nowell & Jackson 1996; Marker & Schumann 1998). Extensive information regarding the feeding ecology of cheetahs has been collected from the Serengeti (Kruuk & Turner 1967; Schaller 1968; Frame 1986; Caro 1994), where 21 prey species were recorded, ranging in size from mole rats (*Cryptomys* spp.) to wildebeest (*Connochaetes taurinus*), with a strong bias towards Thomson's gazelles (*Gazella thomsoni*). Other studies in East Africa (Graham 1966; McLaughlin 1970; Eaton 1974; Burney 1980) have also revealed preferences for gazelles (*Gazella* spp.) and impala (*Aepyceros melampus*), amongst a diverse prey base.

In northern Kenya, cheetahs were observed taking kudu (*Tragelaphus strepsiceros*), gerenuk (*Litocranius walleri*) and dik-dik (*Madoqua kirkii*) (Hamilton 1986), while kob (*Adenota kob*) and oribi (*Ourebia ourebi*) have been noted as prey in West Africa (Nowell & Jackson 1996). Data from the Kafue National Park, Zambia, showed puku (*Kobus vardoni*) to be the favoured prey species (Mitchell *et al.* 1965), while cheetahs in the Lowveld region of South Africa (Hirst 1969; Pienaar 1969) took a preponderance of impala amongst 15 species preyed upon. In the southern Kalahari, Mills (1984) found that cheetahs killed prey ranging from bat-eared foxes (*Otocyon megalotis*) to wildebeest, with springbok (*Antidorcas marsupialis*) as the favoured species.

The summary to date, then, is that cheetahs predominantly kill medium-sized (10–35 kg) antelope, but will opportunistically take other prey if available. Against this background, the diet of cheetahs on Namibian farmlands is interesting for two reasons. First, the cheetahs in this habitat exist in a highly managed ecosystem, where klepto-

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parasites such as spotted hyaenas (*Crocuta crocuta*) and lions (*Panthera leo*) have been eliminated. This is in contrast to previous studies where cheetahs were sympatric with other larger carnivores, where intra-guild competition could be disadvantageous. The investigation of how their dietary preferences change in the absence of such competition would be useful. Second, farmers in Namibia are under the impression that cheetahs kill substantial numbers of domestic stock and ranched game, particularly expensive and exotic game. This had led to a potentially dangerous situation for the Namibian cheetahs as their population is threatened due to their removal by farmers. Cheetahs are known to kill small livestock and calves up to six months of age (Marker-Kraus *et al.* 1996), but it is important to investigate whether the level of predation corroborates the perception of them as a serious problem.

Although classified as protected in Namibia, cheetahs can be shot in order to protect life or property. Namibian farmers have used this exemption as justification to remove cheetahs indiscriminately (Marker-Kraus *et al.* 1996). The majority of the 6829 cheetah removals reported between 1980 and 1991 were described as being necessary to reduce predation on livestock (CITES 1992), although only 2% of the country's farmers reported suffering livestock loss to predators (Marker-Kraus *et al.* 1996). During the 1980s this indiscriminate removal by Namibian farmers was believed to be responsible for more than halving the 6000-strong cheetah population (Morsbach 1987).

Through surveys conducted with Namibian farmers, the cheetah was reported to prey on a wide range of species on the farmlands, including livestock as well as both indigenous and exotic game species (Marker-Kraus *et al.* 1996). This paper aims to identify the relative importance of the different prey species in the diet of cheetahs on Namibian farmlands, so that problems and potential solutions can be identified to develop suitable cheetah conservation strategies.

Diet estimation of carnivorous mammals can be assessed by various methods, each subject to different biases (Mills 1984; Reynolds & Aebischer 1991). Opportunistic and direct observation of kills, while the predominant method for large carnivores in East and South Africa, is impractical in the dense bushveld of Namibian farmland. The traditional solution involves quantification of undigested prey remains in scats (*e.g.* Evermann *et al.* 1988; Previtali *et al.* 1998; Lanszki *et al.* 1999). However, it has long been obvious that extrapolation from volumetric analysis of undigested prey remains in faeces is an unsafe basis for quantifying carnivore diet unless differential digestibility of different prey sizes and species is corrected for (Scott 1941; Lockie 1959; Floyd *et al.* 1978; Ackerman *et al.* 1984). Such uncorrected extrapolation risks, for small prey, the over-estimation of biomass and under-estimation of numbers consumed. Therefore, as one step in our diet analysis we calculated digestibility indices for various prey species of captive cheetahs following the protocol established by Floyd *et al.* (1978) for grey wolves (*Canis lupus*). We then used these indices to estimate rates of livestock predation caused by cheetahs on the farmlands. We also compared estimates of cheetah diet derived by contrasting methodologies (*e.g.* faecal analysis *versus* aerial surveys of kills) to evaluate the biases inherent in each.

METHODS

Feeding trials

Following Floyd *et al.* (1978) we conducted nine trials in two 256 m^2 captive holding pens at the Cheetah Conservation Fund's research farm near Otjiwarongo, Namibia. Before each trial, the cheetahs were fasted until no fresh scats were being produced, a process which took 40–96 hours. This was similar to fasting periods experienced in the wild: Caro (1994) reported fasting times of 30–36 hours, McLaughlin (1970) reported fasts of 48–72 hours, and Broomhall (2001) described fasting periods ranging from 84 to 168 hours.

Carcasses were weighed and then fed intact to the cheetahs. Five carcasses were fed to two wild-born, two-year-old females. Four carcasses were fed to three wild-born, three-year-old males. Four species were used with prey masses <30 kg (hare, *Lepus saxatilis*; lamb, *Ovis aries*; goat, *Capris* sp., and steenbok, *Raphicerus campestris*); while two species were heavier, namely kudu and gemsbok (*Oryx gazella*). Since a high percentage of cheetah kills are either abandoned after gorging or are stolen by a competing predator (Caro 1994), the carcasses were removed when all feeding cheetahs remained lying down for more than 10 minutes without returning to feed (33–125 minutes). After feeding, the carcass was removed and weighed to the nearest 0.5 kg.

Scats were collected twice daily, in order to minimize both trampling and desiccation. Scat consistency varied from liquid or semi-liquid scats that would be unlikely to be found and collected during a field study, which were categorized as non-collectable scats (NC), to firmer scats that were likely to be found and collected in the field (field-collectable, FC). Field-collectable scats were counted and weighed immediately after collection.

Statistical analyses were conducted using SPSS version 10.05 (SPSS, Chicago, Illinois). Kolmogorov-Smirnov and Shapiro-Wilk tests were used to investigate normality, and nonparametric procedures were used where there was significant deviation from normality. Analysis followed Floyd *et al.* (1978) and Weaver (1993), using a least squares regression plot, which yielded a regression equation, where y is the kg of prey consumed per collectable scat and x is the average mass of an individual of a given prey species. By multiplying y by the frequency of occurrence (n) of each prey species in the sample, it was possible to obtain a total mass consumed of each species and calculate the ratios of mass consumed of different prey species. The total mass of each species consumed was then divided by the average estimated mass to compute the number of individuals consumed, and ratios were computed relative to a kudu calf weighing 16 kg. Masses of subadult animals were used for eland (*Taurotragus oryx*), oryx, kudu and red hartebeest (*Alcelaphus buselaphus*), as cheetahs most commonly prey on the calves of these large species rather than adult animals (Marker-Kraus *et al.* 1996).

Scat analysis

Scats were collected from wild cheetahs that were live-trapped by farmers, both from the traps themselves and during examination. Scats were also collected in the field over an area of approximately 18 000 km^2, particularly from 'playtrees', which are trees used by cheetahs for scent-marking with urine and faeces (Marker-Kraus & Kraus 1995).

Scats were individually placed in nylon stockings and washed through two complete regular cycles in a conventional washing machine. No bleach or detergents were used. The washing process left in the stocking only hair, bones, teeth and hooves, and the stockings and their contents were then hung out to dry. The dried remains were spread evenly into a dissecting pan with a grid base comprised of six 67.5 cm^2 squares, and one hair was randomly sampled from each square, carefully examined, and cuticle scale imprints were made.

Hairs were sandwiched between two glass slides on a plastic cover slip, held together by four small (no. 20) binder clips, and heated for five minutes in a toaster oven at 108°C, removed and left to air-cool. The hair was then gently removed from the cover slip using forceps or fingernails, and the hair's scale characteristics were used to determine from which species it originated. Macroscopic distinctions narrowed the options and cuticle imprints finalized the identification. Kudu and eland hairs were often difficult to distinguish so were categorized together in some instances. In compiling our reference collection, we were mindful of Keogh's finding that hair from fresh carcasses and preserved skins are identical (Keogh 1983; Buys & Keogh 1984). Our collection involved hairs and imprints from neck, back, belly and hindquarter regions of each possible prey species in the study area.

Information on kills from radio-tracking flights and farmers

Between 1993 and 1999, radio-collared cheetahs were tracked on a weekly basis from a fixed-wing Cessna 172. During these flights, cheetahs were occasionally sighted on identifiable kills. Although they may do so (Pienaar 1969; Stander 1990; Caro 1994), cheetahs do not generally scavenge from other predators (Wrogemann 1975; Caro 1994) and we therefore assumed that the cheetah had killed the animal being eaten. We also recorded whether the cheetah was sighted within 500 m of livestock or game. Interpretation of the scat analysis data was also made in the context of farmers' answers during a questionnaire survey regarding their observations and perceptions of cheetah predation (Marker-Kraus *et al.* 1996; pers. obs.). The results of the feeding trials and corrected scat analysis were used to estimate rates of livestock predation by cheetahs in the study area.

RESULTS

Feeding trials

Scats containing the presented prey item were produced within 48–111 hours of feeding (Table 1). Of the four smaller prey species, the mean percentage consumed was 69.7%, but for the two species of large antelope this dropped to 16.8%. There was a strong correlation both between prey

Table 1. Results of feeding trials performed on wild-caught, captive Namibian cheetahs. Scats were classified as either field-collectable (FC) or non-collectable (NC) depending on their consistency and likelihood of being collected during a field study.

Prey item	Prey mass (kg)			Mean prey consumed per cheetah (kg)	No. scats produced				Mass of FC scats		Kg of prey consumed/ FC scat	No. FC scats/kg of prey consumed
	Presented	Consumed	Percentage consumed		FC	NC	Total	Total (kg)	% prey mass presented	% prey mass consumed		
Hares (2)*	3.8	3.0	80.0	1.5	9	1	10	0.4	10.9	13.7	0.3	3.0
Lamb	3.8	3.3	86.7	1.6	10	0	10	0.5	14.0	16.2	0.3	3.1
Kudu	109.5	10.0	9.1	5.0	7	6	13	0.9	0.8	8.7	1.4	0.7
Goat	22.5	8.9	39.4	4.4	11	1	12	0.9	4.0	10.2	0.8	1.2
Goat	29.5	10.0	33.9	5.0	10	1	11	1.0	3.3	9.6	1.0	1.0
Goat	28.8	15.1	52.5	5.0	32	8	40	2.2	7.8	14.8	0.5	2.1
Gemsbok	83.5	20.5	24.6	6.8	18	4	22	1.4	1.7	6.9	1.1	0.9
Steenbok	9.3	6.5	70.3	2.2	13	2	15	0.8	8.6	12.2	0.5	2.0
Mean	36.3	9.7	49.6	3.9	13.8	2.9	16.6	1.0	6.4	11.5	0.8	1.8

*Average mass per carcass = 1.88 kg.

mass presented and prey mass consumed (r_s = 0.86, P = 0.007, n = 8), and between prey mass presented and fresh field-collectable scat mass (r_s = 0.74, P = 0.038, n = 8). However, the smaller prey items consumed gave a proportionally greater fresh mass of field-collectable scats in relation to the prey mass presented, with the mass of field-collectable scats averaging 8.1% of the prey mass presented for the four smaller species, but only 1.2% for the kudu and gemsbok. The number of field-collectable scats per kg of food consumed diminished with increased prey mass. The four small species gave an average of 2.4 field-collectable scats per kg of prey eaten, while kudu and gemsbok gave a mean of 0.8 scats/kg.

Data summarized in Table 2 revealed a strong correlation (r = 0.89, P = 0.017, n = 6) between the mass of prey consumed per collectable scat and average mass of the prey species presented. A regression on these variables generated the following equation: $y = 0.0098x + 0.3425$, which can be used to provide valuable information on the relative contribution of different prey species reported as part of the cheetah's diet (Marker-Kraus *et al.* 1996). This information is shown in Table 3.

Scat analysis

Ninety-eight cheetah scats were analysed, of which 79.6% (n = 78) were from cheetahs held for four days or less, and 20.4% (n = 20) were from cheetahs held captive for over four days. From the feeding trial results, only cheetahs that had been captive for four days or less were considered to be indicative of diet in the wild, as any scats produced after this time would not reflect diet before capture. Of the 78 scats from wild cheetahs, 33.3% (n = 26) were from game farms, 48.7% (n = 38) were from livestock farms, and 17.9% (n = 14) were from unknown locations. Table 4 presents the total number of scats collected from wild cheetahs, location of collection and the prey species identified in them. In most cases, the cheetahs appeared to be preying on indigenous game species, while in 6.4% of cases the prey species identified were domestic stock.

Applying corrections for differential digestibility (Table 5), the prey selection can be more accurately determined. Only the scats where kudu and eland hairs could be distinguished were used for those two species. Table 5 highlights the importance of applying correction factors to scat analy-

Table 2. Summary of results from the feeding trials for each prey species presented.

Prey type	Mass of prey (kg)		Percentage	No. scats produced			No. scats per kg prey consumed			Kg prey per FC scat
	Presented	Consumed	consumed	FC	NC	Total	FC	NC	Total	
Hare (2)*	3.8	3.0	80.0	9	1	10	3.0	0.3	3.3	0.3
Lamb	3.8	3.3	86.7	10	0	10	3.1	0.0	3.1	0.3
Steenbok	9.3	6.5	70.3	13	2	15	2.0	0.3	2.3	0.5
Goat (3)**	80.8	34.0	42.1	53	10	63	1.6	0.3	1.9	0.6
Kudu	109.5	10.0	9.1	7	6	13	0.7	0.6	1.3	1.4
Gemsbok	83.5	20.5	24.6	18	4	22	0.9	0.2	1.1	1.1

*Average mass per carcass = 1.88 kg.
**Average mass per carcass = 26.92 kg.

sis to avoid under-representing the consumption of smaller prey animals. For instance, although hare remains were found in only three scats and accounted for only one fifth of the weight represented by kudu, we deduced that nearly twice as many hares as kudu were preyed upon. Conversely, a similar weight of eland and kudu appeared to have been consumed, but use of the correction factor indicated that fewer than half the number of eland would have been killed compared to kudu.

Forty-six scats were analysed from wild cheetahs of known sex (37 from males and nine from females) and identifiable prey remains were found in 27 cases, from 23 male and four female cheetahs. The 46 scats came from 42 different cheetahs (33 males and nine females). A higher percentage of scats from male cheetahs contained the remains of large antelope species (kudu, eland, red hartebeest and gemsbok), while those from females more frequently contained evidence of smaller antelope such as steenbok or duiker (Fig. 1). The remains of domestic stock were found only in scats collected from male cheetahs, but the sample size of scats from female cheetahs was too low to draw any substantial conclusions from this.

Additional information regarding kills

Between 1993 and 1999, 325 visual observations of radio-collared cheetahs were made. From these observations, 21 cases were recorded of cheetahs on identifiable kills, and the prey consumption determined using this method was compared to that from the corrected scat analysis (Fig. 2). Even when limited to the prey species identified through both techniques, the composition of the diet indicated by visual observations and corrected scat analysis differed significantly ($\chi^2 = 33.1$, d.f. = 4, $P < 0.001$). Aerial sightings led to higher representation of kudu, red hartebeest and gemsbok than estimated through the scat analysis, with the other species less well represented. In the instances where cheetahs were located near potential prey (n = 1088 locations), they were within 500 m of game species 77.6% of the time and within 500 m of livestock 22.4% of the time.

From the farm survey conducted, 58.6% (n = 81) of the farmers believed that kudu calves were the primary prey of the cheetah (Marker-Kraus *et al.* 1996). Springbok, where regionally available, were also reported as a main component of the diet, as were warthog (*Phacochoerus aethiopicus*) and steenbok. Gemsbok and hartebeest calves were considered to be common prey, followed by a variety of other animals including duiker (*Sylvicapra grimmia*), eland, ostrich (*Struthio camelus*), small game birds, guinea fowl (*Numida meleagris*), kori bustards (*Ardeotis kori*) and hares.

Estimating rate of livestock predation caused by cheetahs

The maximum rate of food consumption for wild cheetahs has been estimated as 5.5 kg/cheetah/day (Eaton 1974), which equates to 1958 kg of prey consumed/cheetah/year. Our feeding trials revealed that 1.87 field collectable scats were likely to be produced per kilogram of prey consumed, leading to an estimated production of 3661 field-collectable scats/cheetah/year. The scat analysis, although based on a limited sample size, showed that on the Namibian farmlands, 4.3% of scats collected contained evidence of domestic calf consumption, while 2.1% contained sheep remains. Using the correction factor, we calculated a consumption of 0.018 calves for each scat containing calf remains, while the figure was

Table 3. Ratios of prey animals consumed, using the corrected scat analysis, for a theoretical sample of 100 scats containing prey species that have been reported as being part of the Namibian cheetah's diet.

Species	Age class	Assumed mass of prey(kg)[1,2,3]	Prey consumed per scat (kg)	No. of scats	Mass of prey consumed (kg)	Ratio of mass consumed*	No. of individuals consumed	Ratio of no. of individuals consumed*
Kudu	Adult female	200	2.30	100	230.3	4.61	1.15	0.37
	Juvenile	100	1.32	100	132.3	2.65	1.32	0.42
	Calf	16.0	0.50	100	49.9	1.00	3.12	1.00
Red hartebeest	Adult	135	1.67	100	166.6	3.34	1.23	0.40
	Juvenile	67.5	1.00	100	100.4	2.01	1.49	0.48
	Calf	15.0	0.49	100	49.0	0.98	3.26	1.05
Gemsbok	Adult	225	2.55	100	254.8	5.10	1.13	0.36
	Juvenile	113	1.45	100	145.0	2.90	1.28	0.41
	Calf	15.0	0.49	100	49.0	0.98	3.26	1.05
Eland	Juvenile	270	2.99	100	298.9	5.99	1.11	0.35
	Calf	36.0	0.70	100	69.5	1.39	1.93	0.62
Impala	Adult	55	0.88	100	88.2	1.77	1.60	0.51
	Calf	5.5	0.40	100	39.6	0.79	7.21	2.31
Springbok	Adult	39	0.72	100	72.5	1.45	1.86	0.60
	Calf	5.0	0.39	100	39.2	0.78	7.83	2.51
Blesbok	Adult	65	0.98	100	98.0	1.96	1.51	0.48
	Calf	7.0	0.41	100	41.1	0.82	5.87	1.88
Duiker	Adult	18	0.52	100	51.9	1.04	2.88	0.92
	Calf	1.9	0.36	100	36.1	0.72	19.01	6.09
Steenbok	Adult	11	0.45	100	45.0	0.90	4.09	1.31
	Calf	0.9	0.35	100	35.1	0.70	39.04	12.51
Dik-dik	Adult	5	0.39	100	39.2	0.78	7.83	2.51
	Infant	0.8	0.35	100	35.0	0.70	43.79	14.03
Warthog	Piglet	1.2	0.35	100	35.4	0.71	29.52	9.46
Domestic stock	Calf	40	0.73	100	73.5	1.47	1.84	0.59
	Goat	43	0.76	100	76.4	1.53	1.78	0.57
	Sheep	37	0.71	100	70.5	1.41	1.91	0.61
Birds	Ostrich	69	1.02	100	101.9	2.04	1.48	0.47
	Guinea fowl	1.0	0.35	100	35.2	0.71	34.76	11.14
	Kori bustard	14	0.48	100	48.0	0.96	3.43	1.10

[1]Wild mammal mass (Bothma 1989).

[2]Domestic mammal mass (S.B. Deshaies, pers. comm.; Deikmann 2001).

[3]Bird mass (Perrins & Middleton 1985).

*Calculated relative to one kudu calf (16 kg), which was reported as the most common prey item for cheetahs on Namibian farmlands (Marker-Kraus *et al.* 1996).

Table 4. Contents of wild cheetah scats collected from various locations on Namibian farmlands.

	Game farm		Livestock farm		Unknown location in the wild		Overall		% of scats containing identifiable remain	% of scats containing identifiable prey remains
	Total	%	Total	%	Total	%	Total	% of all scats collected		
Total scats collected	26	33.3	38.0	48.7	14	17.9	78	–	–	–
No. with identifiable remains	20	33.3	32.0	53.3	8	13.3	60	76.9	–	–
Cheetah hair only	6	46.2	7.0	53.8	0	0.0	13	16.7	21.7	–
Kudu	2	20.0	8.0	80.0	0	0.0	10	12.8	16.7	21.3
Eland	1	14.3	6.0	85.7	0	0.0	7	9.0	11.7	14.9
Kudu/eland	5	41.7	5.0	41.7	2	16.7	12	15.4	20.0	25.5
Steenbok	3	75.0	1.0	25.0	0	0.0	4	5.1	6.7	8.5
Gemsbok	0	0.0	2.0	100.0	0	0.0	2	2.6	3.3	4.3
Red hartebeest	2	66.7	1.0	33.3	0	0.0	3	3.8	5.0	6.4
Hare	1	33.3	0.0	0.0	2	66.7	3	3.8	5.0	6.4
Bird	0	0.0	0.0	0.0	2	100.0	2	2.6	3.3	4.3
Domestic calf	0	0.0	1.0	50.0	1	50.0	2	2.6	3.3	4.3
Sheep	0	0.0	1.0	100.0	0	0.0	1	1.3	1.7	2.1
Warthog	0	0.0	0.0	0.0	1	100.0	1	1.3	1.7	2.1

0.016 individuals for sheep. Therefore, out of 3661 scats, 157 would be likely to contain calf remains and 77 would contain sheep remains, indicating the consumption of 2.8 calves and 1.2 sheep per cheetah per year. However, Schaller (1972) calculated that cheetahs killed 35% more prey than they consumed, and if this estimate is used, approximate kill rates would be 3.8 calves and 1.6 sheep per cheetah per year. This may be an over-estimate for the Namibian farmlands, however, as the 35% correction factor was derived in the Serengeti, where there is a high level of kleptoparasitism from lions and spotted hyaenas (Schaller 1972). These larger carnivores have been mostly exterminated from the Namibian farmlands, and therefore cheetahs may be able to consume relatively more prey from their kills, lowering the kill-to-consumption ratio.

Assuming a minimum density of 2.5 cheetahs per 1000 km^2 on the farmlands (pers. obs.), and an average farm size of 8000 ha (80 km^2) (pers. obs.), the minimum rate of livestock predation due to cheetahs can be calculated as 0.01 calves and 0.004 sheep per km^2, or 0.76 calves and 0.32 sheep annually on an average-sized farm. The accuracy of these calculations obviously depends on the density of cheetahs living in the study area, estimates of which vary widely (Stander 2001; pers. obs.). Using the highest reported estimates of cheetah density on the Namibian farmlands (34 cheetahs/1000 km^2: Stander 2001), the approximate rates of livestock predation due to cheetahs would be 10.3 calves and 4.4 sheep per farm per year.

DISCUSSION

Conducting these feeding trials and developing a correction factor for cheetahs, which can then be used for analysing scats collected from wild animals, is an important method for improving the accuracy of traditional dietary analysis. The feeding trials supported the conclusions of Lockie (1959) and Floyd *et al.* (1978) that, if analyses are based on uncorrected volumetric measures of undigested remains in scats, then smaller prey items are over-represented in terms of mass but under-represented in numbers. The cheetah is an opportunistic predator whose prey varies in size from rodents to adult ungulates (Schaller 1968; Burney 1980; Frame 1992; Caro 1994; Marker-Kraus *et al.* 1996), and this great variation in prey size makes interpretation of scat analysis more complicated.

Table 5. Ratios of prey animals consumed, calculated using the corrected scat analysis.

Prey type in scats	Assumed mass of prey (kg)*	Prey per scat	No. of scats	Kg eaten	Ratio of mass eaten	No. of individuals eaten	Ratio of no. of individuals eaten
Kudu calf	16	0.50	10	4.99	1	0.31	1
Eland calf	36	0.70	7	4.87	0.97	0.14	0.43
Red hartebeest calf	15.0	0.49	3	1.47	0.29	0.10	0.31
Gemsbok calf	15.0	0.49	2	0.98	0.20	0.07	0.21
Steenbok	11.2	0.45	4	1.81	0.36	0.16	0.52
Domestic calf	40.0	0.73	2	1.47	0.29	0.04	0.12
Domestic sheep	59.0	0.92	1	0.92	0.18	0.02	0.05
Warthog	45.0	0.78	1	0.78	0.16	0.02	0.06
Hare	1.9	0.36	3	1.08	0.22	0.58	1.85

*Assumed adult mass for hare and steenbok but calf for others.

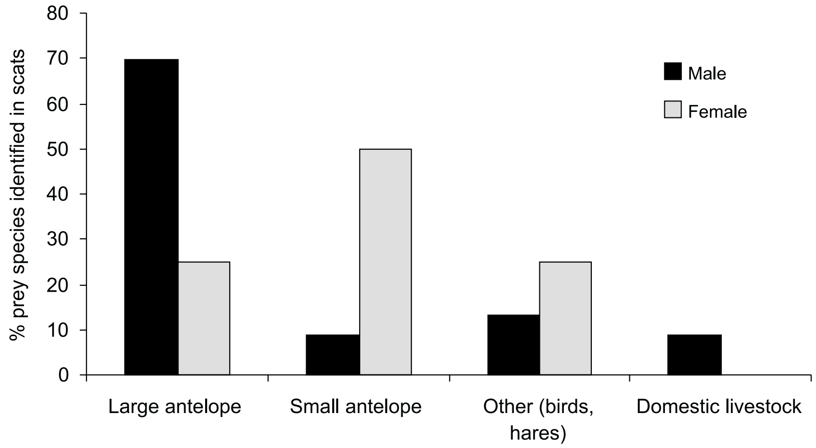

Fig. 1. Percentage of scats from male and female cheetahs that contained remains of large antelope species (*e.g.* eland, red hartebeest, oryx or kudu), small antelope species (*e.g.* steenbok or duiker), other species such as hares and birds, and domestic stock.

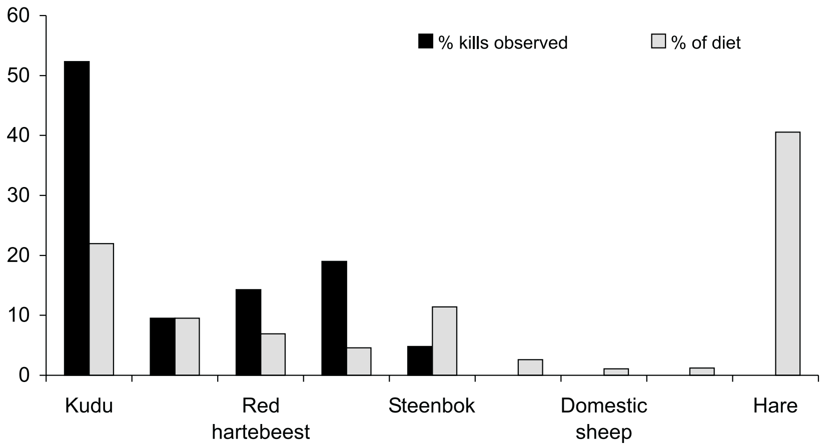

Fig. 2. Estimates of the relative contributions of different prey species to the diet of Namibian cheetahs, using data from observed kills during radio-tracking flights, and from corrected scat analysis.

Consumption of smaller prey gave a higher number of field-collectable scats relative to the mass consumed, because they are composed of relatively more indigestible matter. If this result holds true for other taxa of predators and prey, it is another important bias of scat analysis that should be taken into consideration when the uncorrected technique is used to interpret prey consumption. Feeding on meat alone, rather than bone and hide, tends to result in the production of more liquid scats, and these would probably not be collected during field studies (Floyd *et al.* 1978; Ackerman *et al.* 1984). This is likely to be of particular importance regarding cheetah dietary habits due to their method of prey consumption. Although cheetahs are known to consume some bone (Phillips 1993), they consume more pure muscle (rather than skin or bone) than do other large carnivores (Wrogemann 1975; van Valkenburgh 1996), and this is likely to be even more pronounced when eating from a large carcass. Use of correction factors is therefore very important for accurately estimating cheetah diets. One caveat, however, is that in this study we followed the protocol used by Floyd *et al.* (1978), but in future studies we feel that it would be useful to do more extensive feeding trials for improved accuracy. Our results showed some important variation in factors such as the mass of prey consumed per field-collectable scat for the same prey species (*e.g.* goats), and further trials would be useful to quantify such factors with greater precision.

Accurate analysis of wild cheetah diet relies on the collection of enough scats from which prey remains can be identified. Using the equations in Reynolds & Aebischer (1991), 9600 scats containing identifiable prey remains would be required to establish that these estimated prey proportions are accurate. Given that only 76.9% of the wild cheetah scats analysed contained identifiable prey remains, it would necessitate 12 500 scats to achieve the aforementioned statistical power. Our experience has shown that collecting cheetah scats is very difficult due to several factors, including large home ranges (Marker 2000) and the rapid desiccation of scats in arid environments. In addition, scats are difficult to collect from cheetahs trapped by farmers, as the cats have often gone without food for several days, and any scats produced while in the traps are frequently trampled. The available data, therefore, based on a much smaller sample size, can only give a basic insight into the dietary habits of cheetahs on Namibian farmlands. Collecting scats from 'playtrees' and trapped cheetahs biases the data towards males, as the majority of cheetahs visiting playtrees and being trapped are male (Marker-Kraus & Kraus 1995; Marker-Kraus *et al.* 1996). Male cheetahs are likely to take larger prey than females (Mills 1992), so the prey selection determined during this study may not be entirely representative of female cheetahs. In addition, the interpretation of the scat analysis in terms of numbers of prey animals consumed assumes that the prey animals taken weighed approximately the average masses shown. However, despite these limitations, and especially given the lack of other information, these data can contribute usefully to understanding the diet of wild Namibian cheetahs on farmlands.

The radio-tracking data revealed that cheetahs were sighted near livestock relatively frequently, and this was exacerbated by the species' diurnal nature and consequently greater visibility than other predators. Such sightings by farmers who were experiencing stock loss potentially led to the assumption that cheetahs were the cause, and created the perception of them as being frequent stock-killers. The corrected scat analysis indicated, however, that cheetahs preferentially took wild game species over domestic ones. Although 38 scats were collected on livestock farms (over half from cheetahs that had been trapped as a supposed threat to livestock), only two of those contained any evidence of domestic stock consumption. The fact that domestic stock was evident in 6.4% of the scats does verify that cheetahs prey on livestock, but as two-thirds of the available prey base is livestock (Marker-Kraus *et al.* 1996) cheetahs appear to show selection towards game species.

It is difficult to estimate rates of livestock predation due to cheetahs from this information, as estimated figures for cheetah density in the study area vary greatly (Marker *et al.,* pers. obs.; Stander 2001). In a recent survey (pers. obs.), farmers in the region reported losing an average of 0.9 calves and 1.3 small livestock annually to cheetahs, which was slightly higher than estimated using the minimum density figures, but far less than would be expected if cheetahs existed at maximum density. Conducting further research in order to gain a more accurate estimate of cheetah density will be vital for independently examining the level of stock loss that cheetahs are likely to be responsible for. Relying therefore on reports by farmers, the level of livestock predation attributed to cheetahs was substantially less than that caused by other predators, and indicate that livestock predation due to cheetahs is unlikely to be a major financial burden for Namibia's commercial farmers (pers. obs.).

However, the predominance of game species in the diet does mean that the cheetah is likely to be perceived as a threat on game farms. Many game farmers stock exotic game species on their land for trophy hunters, and these animals are more valuable economically than indigenous game but can be more liable to predation than the better-adapted indigenous species (Marker-Kraus *et al.* 1996; Marker & Schumann 1998). Although these results suggest that cheetahs are preying mainly on indigenous game species rather than the more expensive exotic game, losses to large carnivores remain a potential problem for game farmers.

In line with comparable studies of other carnivores (*e.g.* Mills 1992; Karanth & Sunquist 1995), the diet estimated from sighted kills contained a greater proportion of large prey than did that estimated from faeces. The only exception in this study was for eland, where fewer kills were seen than would be expected from the scat analysis. This may be due to the fact that eland are nomadic (Smithers 1983) and for much of the time would not be on farmland where radio-tracked cheetahs were being followed.

The wild prey base available to the cheetah is critical in the issue of predator conflict. According to many Namibian farmers, maintaining a substantial population of wild game is the most important feature in reducing livestock predation in the survey area (Marker-Kraus *et al.* 1996), as a plentiful wildlife population provides an abundance of prey, which in turn reduces the farmers' conflict with predators. However, even a relatively low level of predation on expensive, introduced game, or on livestock, can have economic impacts on farmers that they are unwilling to tolerate (Oli *et al.* 1994). Therefore, in order to conserve cheetahs successfully on farmlands and reduce the level of removal, strategies must be found that mitigate such economic losses. Fenced sections of farms, containing expensive game animals, can be protected through effective maintenance of perimeter fences or erecting an electric fence, or, more sustainably, by the removal of game fencing and the development instead of cooperative game management areas in the form of conservancies. There are also several livestock management practices, such as the use of guarding animals, calving corrals and synchronized breeding seasons, that have been shown to be effective in reducing stock losses both to cheetahs and other predators (Marker-Kraus *et al.* 1996). In addition, the development of ecotourism and sustainable trophy hunting both have the potential to turn predators into an economic asset rather than a detriment to the farmers on whose lands they survive.

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