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Health of adult free-living cheetahs

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Health of free-living adult cheetahs was assessed using haematological and biochemical measurements of condition. Results showed that cheetahs of both sexes varied on several of these measures, demonstrating that their genetic monomorphism does not result in individuals being of equivalent health. Differences in condition appeared to be somewhat associated with sex, age and whether males were territorial. Compared to two different groups of captive cheetahs, free-living cheetahs were monocytotic, and free-living females were macrocytic. Limited data from captive animals showed they ate more than their free-living counterparts, possibly reflecting the elevated blood glucose levels of captive cheetahs.

Contents

Introduction

Both Southern African cheetahs (*Acinonyx jubatus*) (O'Brien *et al.*, 1983) and East African cheetahs (O'Brien *et al.*, 1987) are unusual among felids and other mammals in having extreme paucity of genetic variation, as estimated by electrophoretic surveys of allozymes and cell proteins resolved by two-dimensional gels. More unusual was the observation that 14 cheetahs accepted allogenic skin grafts from unrelated cheetahs, revealing genetic monomorphism at the major histocompatibility complex, an abundantly polymorphic locus in nearly all mammals (O'Brien *et al.*, 1985). This lack of genetic variability raises questions about the ability of cheetahs to combat the challenge of infectious diseases. For example, feline infectious peritonitis resulted in the death of 50% of the cheetahs in a highly successful captive breeding programme at the Wildlife Safari,

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Oregon, USA (L. Marker, pers. comm.), while none of the exposed lions (*Panthera leo*) developed disease symptoms. To date, however, we have no knowledge of whether free-living cheetahs are either equally susceptible or resistant to diseases as their genetic monomorphism might imply, or whether their genetic homogeneity results in a high variance in condition because of reduced genetic buffering in the face of environmental perturbations. Unfortunately, personnel involved in capturing animals for zoological gardens or big game hunters did not, for economic or social reasons (Caro, 1984), systematically record symptoms of ill-health in their specimens (but see Loveridge, 1933).

Habitat destruction is considered to be the primary cause of the present decline in cheetah numbers (Myers, 1975), now thought to number no more than 25,000 in the wild (Frame, 1984); and where they do occur, cheetah distribution is known to be somewhat constrained by local topography (Caro & Collins, 1987*a*). In addition, mortality among males is high (McVittie, 1979; Caro & Collins, 1986), and cheetahs suffer from interspecific competition with other predators (Bertram, 1979; Frame, 1986). Their diurnal hunting makes them particularly likely to lose prey through the activities of their cubs (Caro, 1987), and to be harassed by tourists visiting national parks in which many now live (Henry, 1977; Caro, 1986). All these facts make it clear that captive breeding programmes are likely to assume increasing importance in the fate of this species. Such programmes could profit from baseline haematological and biochemical data, so that abnormal clinical conditions can be identified and appropriate changes in management made to improve the chances of successful breeding.

In this paper, we first present quantitative data on the health and condition of 17 wild cheetahs, living in one of their last viable strongholds, the Serengeti National Park, Tanzania, in order to determine whether free-living individual cheetahs are equally healthy or in very different condition, both of which might be predicted by their genetic uniformity. Secondly, we compare these data with two independent samples of normal captive adult cheetahs, from Britain (see also Hawkey & Hart, 1986) and from the USA (ISIS, 1984), to determine whether haematology and clinical chemistry of captive specimens differ from their free-living counterparts.

Methods

Seventeen adult cheetahs (10 males and 7 females) were darted using a handheld blowpipe from a landrover as part of a long-term radio collaring programme. Habituated animals that were not shy of the vehicle were approached to within 10 m, and a 3 ml mini-ject syringe (3064 Dist-inject) with 1·5 × 30 mm (K153OV Telinject) needle and tailpiece (Zoolu arms of Omaha) containing 1–1·5 ml tiletamine hydrochloride and zolazepam hydrochloride at a concentration of 200 mg/ml (Zoletil, Virbac) was shot at the animal's hind quarters using lung pressure alone. Struck animals normally ran about 30–50 m but then quickly settled down and showed signs of sedation within 3–5 min, and were recumbent within 10 min; they were not followed by the vehicle. When the individual had lain down for approximately 2 min, the vehicle approached, and a 10 ml blood sample was taken from the cephalic vein. This was done immediately to avoid the problem of changes in red blood cell parameters that occur after the onset of anaesthesia in this species (Hawkey *et al.*, 1980). Two and a half ml of blood were mixed with dipotassium salt of ethylene diamine tetracetic acid (2K EDTA), while the remaining 7·5 ml was allowed to clot. All blood samples were placed in a coolbox at approximately 0°C. Individuals then received a physical examination. In addition, 3 measures of general condition were scored. First, the ease with which the dorsal spinous process vertebrae could be palpated was recorded (1: easily palpable; 2: palpable with moderate pressure; 3: palpable with strong pressure). Secondly, coat quality was recorded as soft (s), or coarse (c). Thirdly, the degree of mange on each ear was recorded (0, none; 1, tips of ears only; through to 5, severe, where the entire pinnae were involved). Faecal samples were collected. The

bladder was palpated but too few urine samples were obtained to provide useful results. After the animal was weighed and measured, and, in some cases, a radio collar fitted, the observers retreated to the vehicle and waited until the cheetah had recovered sufficiently to avoid dangerous predators such as lions or spotted hyaenas (*Crocuta crocuta*).

Samples were then taken back to the laboratory. Total red and white cell numbers were counted by standard techniques using a Neubauer counting chamber (Dacie & Lewis, 1984). Packed cell volumes and haemoglobin concentrations were measured using Microcompur minicentrifuges. Blood smears were made, air dried, fixed in methanol, stained with Giesma stain, and a differential white cell count was performed. Differential white cell counts were reasonably consistent between observers: MEH and CMH differed by an average of 4·2% (S.D. = 5·0) when the 5 types of white blood cell from 5 different animals were independently counted. Stained slides were also examined for evidence of blood-borne parasites. Serum samples were heat inactivated at 57 °C for 20 min, and returned to UK under licence for biochemical analysis. Faecal samples were mixed with saturated salt solution, and egg counts performed using the modified MacMaster technique.

In addition to this sample, blood sera collected using exactly the same procedure as above, and stored and treated in the same way, were available from 8 male and 6 female cheetahs living in the Serengeti ecosystem (both Tanzania and Kenya), as were sera from 3 captive East African cheetahs housed in Kenya. Biochemical data from these animals are presented in a separate table in order to increase the sample size.

Comparisons between the sexes were made using Mann-Whitney U tests (2-tailed) as sample sizes were small (Siegel, 1956), while those comparing animals of different age and status were based on qualitative comparisons as few individuals were involved. Raw values are presented here together with the summary statistics, so that individual differences pointed out in the text can be examined.

Results

Table I presents individual weights, linear measurements and measures of body condition for the free-living sample. Males weighed slightly more than females but the difference was not significant ($U=9$, ns). Linear measurements for males and females did not differ significantly from each other except that female tail lengths were somewhat shorter than those of males ($U=11·5$, $P<0·1$, omitting female 3; otherwise from left to right across the Table, $U=28·5$, 18, 27·5, comparing the average length of the two upper canines, all ns). Similarly, no sex differences were found on the two measures of body condition that were scored (vertebrae, $U=24$, ns; mange, $U=29$, ns). Male 17 appeared to be in very poor condition compared to other males. He had widespread severe mange and dermatitis, and gingivitis and ulcerations in his mouth; also all superficial lymph nodes palpated were enlarged. Interestingly, male 5, the only male that was known to be territorial at the time (Caro & Collins, 1987*b*), was over 5 kg heavier, and was in better condition, as measured by vertebral palpation and coat, than other males.

Table II gives haematological values for the free-living sample. Females had slightly higher mean cell volumes (MCV) ($U=14$, $P<0·1$) than males (results from female 1 were discarded from this comparison as her red blood cell count (RBC) may have been incorrect). There were no significant sex differences in red cell counts ($U=14·5$), packed cell volumes (PCV) ($U=21·5$), white blood cell counts (WBC) ($U=31·5$), or most differential white cell counts (neotrophils percentages $U=23$, real values $U=30$; lymphocytes $U=29·5$, 34; monocytes $U=23$, 30; eosinophils $U=16·5$ ($P<0·1$), 27; basophils $U=32·5$, 32, all ns), except that males showed a somewhat higher percentage of eosinophils than females (male 12's basophil count may have been inflated due to staining problems). Female 3 was sampled twice, 18 days apart, and haematological values on the first occasion (given in Table II) corresponded well with those taken on the second occasion (respectively, across the Table: 5·0, 0·32, 64, 7·6, 66%, 22%, 5%, 7%, 0%), indicating that the

TABLE 1

Weights and measures (in cm) of 17 free-living cheetahs

Identity	Wt (kg)	Nose–anus	Tail	Hind foot	Canines R	Canines L	Vertebrae	Coat	Mange	Status	Comments
MALES											
5	52·0	122	71	30	2·1	2·2	3	S	1	Territorial adult	4 ticks
6	39·5	125	66	29	2·4	2·4	2	C	3/4	Non-territorial adult	Lower incisor & end of tongue missing
7	45·5	127	71	29	2·0	2·0	2	C	1	Subsequently territorial	14 ticks
8	40·5	123	69	27	2·1	2·0	1	C	2	Subsequently territorial	4 ticks
11	46·5	129	66	29	–	–	1	C	2	Old, formerly territorial	Loss of chest hair, 14 ticks, inflamed gums
12	–	121	69	27	2·1	2·1	2	?	1	Non-territorial young adult	10 ticks
13	33·5	108	64	25	2·0	2·0	2	S	0	Non-territorial young adult	N.A.D.
14	45·0	128	69	28	2·1	2·1	2	S	0	Non-territorial adult	Slightly infected gums, 16 ticks
17	36·5	126	69	28	2·3	2·2	1·5	C	4	Non-territorial adult	Very poor condition*
18	41·5	124	69	28	2·1	2·0	2	S	0	Non-territorial adult	12 ticks
Mean	42·3	123·3	68·3	28·0	2·12		1·9		1·5		
S.D.	(5·6)	(6·0)	(2·3)	(1·4)	(0·13)		(0·6)		(1·4)		
FEMALES											
1	42·0	–	64	27	2·1	2·1	2·5	S	0	Adult	Ulcerated upper gum
2	40·0	190	69	26	1·9	2·0	2	C	2	Adult	N.A.D.
3	33·0	140	54	27	2·1	2·1	1	C	4	Old	35 ticks
4	34·0	122	66	27	2·1	2·1	2·5	C	2	Adult	26 ticks
10	43·0	125	67	28	2·0	2·0	2·5	?	2	Adult lactating	8 ticks
15	31·5	113	61	27	2·1	2·0	2	C	1	Young adult	13 ticks
16	41·5	122	64	28	2·1	2·2	2	S	1	Young adult pregnant	9 ticks
Mean	37·9	135·3	63·6	27·1	2·06		2·1		1·7		
S.D.	(4·8)	(28·2)	(4·9)	(0·7)	(0·07)		(0·5)		(1·3)		
G. mean	40·3	127·8	66·4	27·6	2·10		1·9		1·6		
S.D.	(5·6)	(18·0)	(4·2)	(1·2)	(0·11)		(0·6)		(1·3)		

* No. 17 had mange on a shoulder, elbows and footpads; sebaceous exudate in groin, erythromatous lesions on chest and extensive hair loss; lymph nodes were enlarged. No. 3 had part of her tail missing.

values presented were consistent over time. Male 17 was anaemic, with a low red blood cell count and an increased number of neutrophils, lymphocytes, monocytes and eosinophils compared to other males, which was reflected in his very high total white cell count. Old male 11 had a low red blood cell count, and males 6 and 7 had eosinophilia. No blood-borne parasites were found on any of the smears examined.

Table III compares these data with those of two groups of captive animals. The red cell counts of free-living female cheetahs were considerably lower and the red cells were macrocytic compared with both captive male and captive female animals. The limited data on haemoglobin levels shows they were similar to captive animals. The variation in total white cell count was greater in free-living than in captive cheetahs in both males and females, and the percentage of monocytes was higher than in their captive counterparts.

Table IV gives the values of biochemical analyses for the blood of free-living cheetahs. There were few significant differences between the sexes (respectively, across the Table: $U = 25{\cdot}5$, 28·5, 28·5, 26·5, 21·0, 28·0, 34·5, all ns) except that females showed somewhat higher levels of magnesium than males ($U = 16$, $P < 0{\cdot}1$). Biochemical values for female 3's second sample were similar to the first, shown in the Table. They were urea 11·4, glucose 5·7, creatinine 179, chloride 130, calcium 2·96 and magnesium 1·50; no values were available for sodium or potassium. The elevated glucose value compared to the first sample might have been attributable to this animal having fed relatively recently.

Table V provides additional data on these measures from a sample of free-living cheetahs collected earlier in the same location. These data show that urea levels in females tended to be slightly higher than in males ($U = 10$, $P < 0{\cdot}1$). Females had significantly lower chloride values than males in this sample ($U = 4$, $P < 0{\cdot}01$); (other measures $U = 17$, 18·5, 16·5, 22, 17, 21·5, all ns, respectively, across the Table). (Creatinine values differed widely in the two free-living samples for unknown reasons: slight differences in how analyses were performed, or that the earlier sample was taken in the dry season, the latter in the wet, are two possibilities.)

Biochemical values of free-living cheetahs are compared to those of captive animals in Table VI. Blood urea values in the two groups were similar, however, blood glucose levels were considerably higher in the ISIS captive sample of cheetahs. Similarly, creatinine levels in the 'British' and ISIS captive samples were noticeably higher than in either of the free-living samples. Sodium, potassium, chloride and calcium levels were comparable to captive groups.

Faecal samples from three of the five females, and seven of eight free-living males contained between one and 17 *Ancylostoma* eggs. A *Dipylidium* tapeworm segment was found in one faecal sample from a female. The mange found on many of the free-living cheetahs was sarcoptic mange as identified by microscopic examination of skin scrapings. Every animal had a number of hippoboscid flies which collected on their ventral surface.

Discussion

Variation in the health of cheetahs

Data presented here show that, in spite of their genetic uniformity (O'Brien *et al.*, 1983, 1987), free-living cheetahs varied considerably in their condition. Our three measures of condition all confirmed that female 1, and males 5, 13, 14 and 18 were all in good health, whereas the other cheetahs had coarse coats, prominent or discernible vertebral processes, and suffered from varying degrees of sarcoptic mange and tick infestation. In general, females were in better condition than

TABLE II

Haematological reference values for adult free-living cheetahs

	Identity	Hb (g/dl)	RBC ($\times 10^{12}$/l)	PCV (l/l)	MCV (fl)	WBC ($\times 10^9$/l)	Neutro. % ($\times 10^9$/l)	Lympho. % ($\times 10^9$/l)	Mono. % ($\times 10^9$/l)	Eosin. % ($\times 10^9$/l)	Baso. % ($\times 10^9$/l)
MALES	5		9·1	0·44	48	15·0	83	11	2	4	0
							12·45	1·65	0·30	0·60	0
	6		8·0	0·42	53	10·0	53	19	7	21	0
							5·30	1·90	0·70	2·10	0
	7		7·4	0·33	45	11·8	68	17	3	12	1
							8·02	2·00	0·35	1·42	0·12
	8		7·1	0·36	51	9·6	76	16	4	4	0
							7·30	1·54	0·38	0·38	0
	11		4·5	0·21	47	10·8	68	23	1	8	0
							7·34	2·48	0·11	0·86	0
	12		8·0	0·42	53	12·4	62	26	3	6	3
							7·69	3·22	0·37	0·74	0·37
	13		5·5	0·32	58	14·3	65	25	2	8	0
							9·30	3·58	0·29	1·14	0
	14	12·6	7·3	0·37	51	8·1	60	29	5	7	0
							4·86	2·35	0·41	0·57	0
	17	10·6	4·1	0·30	73	26·8	67	21	4	9	0
							17·96	5·63	1·07	2·41	0
	18	13·5	11·4	0·38	33	9·8	68	23	1	8	0
							6·66	2·25	0·10	0·78	0
Mean		12·2	7·2	0·36	51·2	12·9	67·0	21·0	3·2	8·7	0·4
S.D.		(1·5)	(2·2)	(0·07)	(10·1)	(5·3)	(8·3)	(5·4)	(1·9)	(4·9)	(1·0)
Mean							8·69	2·66	0·41	1·10	0·05
S.D.							(3·89)	(1·23)	(0·29)	(0·68)	(0·12)
FEMALES	1		2·2	0·32	145	12·2	75	16	2	7	0
							9·15	1·95	0·24	0·85	0
	2		5·3	0·30	57	12·4	77	13	2	7	0
							9·55	1·61	0·28	0·87	0
	3		4·8	0·33	69	8·4	68	21	4	7	1
							5·71	1·76	0·34	0·59	0·08
	4		4·4	0·34	77	15·6	68	24	2	6	0
							10·61	3·74	0·31	0·94	0
	10		4·9	0·31	63	6·0	70	27	2	1	0
							4·20	1·62	0·12	0·06	0
	15	12·6	7·3	0·30	41	14·2	57	36	1	6	0
							8·09	5·11	0·14	0·85	0
	16	13·3	5·8	0·38	66	15·7	69	25	2	4	0
							10·80	3·93	0·31	0·63	0
Mean		13·0	5·0	0·33	74	12·1	69·1	23·1	2·1	5·4	0·1
S.D.							(6·4)	(7·6)	(0·9)	(2·2)	(0·4)
Mean							8·30	2·82	0·25	0·68	0·01
S.D.							(2·50)	(1·42)	(0·09)	(0·30)	(0·03)
G. Mean		12·5	6·3	0·34	60·6	12·5	67·9	21·9	2·8	7·4	0·3
S.D.		(1·1)	(2·2)	(0·06)	(24·6)	(4·6)	(7·4)	(6·2)	(1·6)	(4·3)	(0·8)
G. Mean							8·53	2·72	0·34	0·93	0·03
S.D.							(3·30)	(1·27)	(0·24)	(0·58)	(0·09)

most of the males. Indeed, one old male (No. 11) was apparently anaemic and had severe gingivitis and dermatitis on his chest, while male 17 was anaemic and had a high white cell count; he had been observed to contract mange within a period of 18 months (A. Collins, pers. comm.). These findings

TABLE III

Means and (standard deviations) of haematological reference values for adult male (n = 10) and adult female (n = 7) free-living and captive cheetahs (males, n = 10; females, n = 12). n and S.D.s for adult ISIS sample not available. RBC and MCV values for female 1 were omitted (see text)

	Hb (g/dl)	RBC ($\times 10^{12}$/l)	PCV (l/l)	MCV (fl)	WBC ($\times 10^9$/l)	Neutro. % ($\times 10^9$/l)	Lympho. % ($\times 10^9$/l)	Mono. % ($\times 10^9$/l)	Eosin. % ($\times 10^9$/l)	Baso. % ($\times 10^9$/l)
Free-living sample (this study)										
Males	12·2	7·2	0·36	51·2	12·9	67·0	21·0	3·2	8·7	0·4
	(1·5)	(0·2)	(0·07)	(10·1)	(5·3)	(8·3)	(5·4)	(1·9)	(4·9)	(1·0)
						8·69	2·66	0·41	1·10	0·05
						(3·89)	(1·23)	(0·29)	(0·68)	(0·12)
Females	13·0	5·0	0·33	74·0	12·1	69·1	23·1	2·1	5·4	0·1
	(0·5)	(1·5)	(0·03)	(33·3)	(3·7)	(6·4)	(7·6)	(0·9)	(2·2)	(0·4)
						8·30	2·82	0·25	0·68	0·01
						(2·50)	(1·42)	(0·09)	(0·30)	(0·03)
Captive 'British' sample (Hawkey, unpubl. data)										
Males	13·4	7·4	0·37	52·7	10·9	73·0	17·0	0·6	9·4	Rare
	(1·5)	(0·8)	(0·04)	(1·7)	(1·2)	(7·0)	(6·0)	(0·5)	(1·6)	
						7·96	1·83	0·08	0·94	
						(1·63)	(0·50)	(0·07)	(0·07)	
Females	13·9	7·0	0·41	57·7	8·2	67·0	21·0	1·2	10·8	Rare
						(5·0)	(6·0)	(1·2)	(2·9)	
						5·63	1·74	0·10	0·91	
						(0·71)	(0·51)	(0·10)	(0·33)	
Captive 'ISIS' sample (1984)										
Males	14·1	7·7		54·0	11·6					
	–	–		–	–					
						6·50	2·60			
						–	–			
Females	12·6	6·9		55·2	11·5					
	–	–		–	–					
						4·10	2·00			
						–	–			

support previous observations made, at a distance, of a number of cheetahs in the Serengeti suffering from mange, at least on their ears. In two of these additional examples, mange was particularly severe: a large male cub, still dependent on its mother, had mange covering its ears, face and neck, and a large abscess of about 8 cm diameter on its haunch; while a second male, a member of a sibling group, was also heavily infested. Although these two individuals may have had congenital defects because their hind legs were swollen and they had difficulty in walking, it is interesting to note that both of these males, and male 17 as well, were young when they contracted mange, a time when they may be under particular stress in trying to avoid harassment from older, and larger territorial males (Caro & Collins, 1987*b*). All Serengeti cheetahs may suffer from a degree of mange in old age but it is unknown if this differs from other populations (see Murray, 1967).

Variation in condition of free-living cheetahs was in part associated with age: female 3 and male 11 were known from demographic records to be a minimum of eight years old and were in poor condition. Variation in condition was also associated with sex. By comparison with free-living males and with findings on captive males and females, the red cells of free-living females were

TABLE IV

Biochemical data from the blood of free-living cheetahs in S.I. Units

Identity	Urea (mmol/l)	Glucose (mmol/l)	Creatinine (μmol/l)	Sodium (mmol/l)	Potassium (mmol/l)	Chloride (mmol/l)	Calcium (mmol/l)	Magnesium (mmol/l)
MALES								
5	10·6	3·5	105	185	3·6	94	1·4	0·9
6	11·0	2·8	66	145	3·7	96	2·0	0·8
7	11·8	4·6	61	178	3·6	106	1·8	0·9
8	13·6	3·0	24	180	3·6	106	2·5	1·1
11	13·6	6·8	78	152	3·5	121	2·4	0·9
12	16·5	5·1	132	160	3·8	122	2·7	0·8
13	12·2	3·4	169	157	4·5	130*	2·6	0·9
14	15·5	6·2	153	158	3·7	120	2·7	1·0
17	7·9	3·0	152	160	4·4	122	2·5	0·9
18	10·8	5·2	130	156	4·3	119	2·6	0·9
Mean	12·4	4·4	107·0	163·1	3·9	113·6	2·3	0·9
S.D.	(2·5)	(1·4)	(47·9)	(13·2)	(0·4)	(12·2)	(0·4)	(0·1)
FEMALES								
1	13·8	4·5	75	151	3·6	96	1·8	0·9
2	14·1	4·4	63	156	3·8	103	2·0	1·0
3	13·0	5·1	68	154	4·0	100	2·0	1·0
4	16·1	4·1	–	172	4·5	130	3·0	1·5
10	14·8	5·4	124	176	4·1	104	2·3	0·9
15	11·8	5·0	132	155	4·6	119	2·9	1·0
16	10·5	4·9	156	159	4·4	121	2·6	1·0
Mean	13·4	4·8	103·0	160·4	4·1	110·4	2·4	1·0
S.D.	(1·9)	(0·5)	(39·2)	(9·6)	(0·4)	(12·8)	(0·5)	(0·2)
G. Mean	12·8	4·5	105·5	162·0	4·0	112·3	2·3	1·0
S.D.	(2·3)	(1·1)	(43·5)	(11·6)	(0·4)	(12·2)	(0·4)	(0·2)

* Score probably inflated due to lysis

macrocytic (mean cell volumes of females in the captive 'British' sample were also significantly larger than in males ($P<0·01$); Hawkey, unpubl. data). No sex differences were found in white blood cell counts of free-living cheetahs, whereas captive males had significantly higher total white blood cell counts ($P<0·001$) and neutrophil counts ($P<0·001$) than captive females (Hawkey, unpubl. data). However, this may have been due to one or two captive males having counts, associated with a recent challenge of infection. A further sex difference was found in biochemical measures, with free-living females from one of the samples having somewhat higher levels of blood urea than males, perhaps indicating that they had a better diet, or had some impairment of kidney function resulting in a reduced rate of excretion of this compound. Lastly, in males, there was limited evidence to suggest that territoriality and good condition were associated, reflecting differences in weight and health of territorial and non-territorial males noted earlier (Caro & Collins, 1987*b*).

Variation in the condition of free-living animals, for example the macrocytosis in females and the eosinophilia in some males, suggests that individuals might have been differentially exposed to disease at the time of sampling. However, current knowledge of the movement patterns of both male and female cheetahs in the Serengeti National Park indicates that there are no geographically

TABLE V

Biochemical data from the blood of free-living cheetahs in S.I. units (Bush, unpubl. data). Parentheses indicate three animals captive in Kenya; means and standard deviations are for free-living sample only

	Urea (mmol/l)	Glucose (mmol/l)	Creatinine (μmol/l)	Sodium (mmol/l)	Potassium (mmol/l)	Chloride (mmol/l)	Calcium (mmol/l)	Magnesium (mmol/l)
MALES								
	19·6	5·5	114	156	4·6	112	2·3	0·9
	9·6	6·5	220	159	4·7	110	2·5	1·0
	10·4	5·3	167	166	5·5	112	2·5	1·1
	18·9	7·2	123	162	4·9	120	2·6	0·9
	14·6	6·5	150	157	4·3	112	2·3	0·8
	10·4	6·5	202	155	4·1	111	2·1	0·8
	12·1	6·2	255	162	4·7	114	2·6	0·8
	12·5	6·1	211	160	4·4	112	2·4	0·9
	(16·1)	(5·9)	(114)	(163)	(4·5)	(115)	(2·5)	(0·9)
	(15·7)	(5·8)	(106)	(167)	(5·0)	(–)	(3·0)	(1·4)
Mean	13·5	6·2	180·3	159·6	4·7	112·9	2·4	0·9
S.D.	(3·9)	(0·6)	(49·8)	(3·7)	(0·4)	(3·1)	(0·2)	(0·1)
FEMALES								
	17·5	6·2	176	160	5·2	110	2·6	0·8
	16·4	5·2	150	157	4·6	111	2·3	0·8
	15·4	6·2	150	155	4·7	114	2·3	0·9
	15·4	6·9	264	158	4·7	109	2·3	1·2
	16·4	5·7	97	150	4·1	102	2·1	0·9
	22·5	5·4	123	162	4·7	110	2·4	0·8
	(16·8)	(5·2)	(167)	(163)	(4·4)	(115)	(2·4)	(0·8)
Mean	17·3	5·9	160·0	157·0	4·7	92·7	2·3	0·9
S.D.	(2·7)	(0·6)	(57·6)	(4·2)	(0·4)	(38·7)	(0·2)	(0·2)
G. Mean	15·1	6·1	171·6	158·5	4·7	111·4	2·4	0·9
S.D.	(3·8)	(0·6)	(52·2)	(4·0)	(0·4)	(3·8)	(0·2)	(0·1)

distinct subpopulations which might restrict the spread of disease. Females and their cubs, and non-territorial males, migrate annually from the Plains to the woodland border where they collect during the dry season (Frame, 1984), and territorial males encounter other cheetahs both on their territories and when they periodically vacate them (Caro & Collins, 1987*a*). Also, no significant variation was found in either enteric or blood-borne parasite loads, suggesting similar exposure between individuals.

It is more likely that differences in condition were associated with differences in age, past exposure to pathogens, sex, nutritional state and stress, all of which are known to affect the immune response. Thus, although genetic monomorphism could be an influential factor in reducing the variability in cheetahs' response to disease, numerous other factors also appear to be important in increasing the variation, as this study has indicated. Furthermore, it is conceivable that individuals may also differ genetically in their ability to resist infection if alleles concerned with condition and disease resistance were not among the homozygous alleles sampled by O'Brien *et al.* (1983, 1987). However, it is unknown whether the genetic homozygosity of East African cheetahs is an additional influence increasing individual variation in condition because of the possible impaired ability of the genome to buffer the effects of environmental factors described above.

TABLE VI

Means and (standard deviations) of biochemical data from free-living (males, n = 10, females, n = 7, this study; males, n = 8, females, n = 6, Bush unpubl. data) and adult captive (males, n = 8, females, n = 7) cheetahs. n and S.D.s for adult ISIS sample not available. Only six creatinine values available from females in this study

	Urea (mmol/l)	Glucose (mmol/l)	Creatinine (μmol/l)	Sodium (mmol/l)	Potassium (mmol/l)	Chloride (mmol/l)	Calcium (mmol/l)	Magnesium (mmol/l)
Free-living sample (this study)								
MALES	12·4	4·4	107·0	163·1	3·9	113·6	2·3	0·9
	(2·5)	(1·4)	(47·9)	(13·2)	(0·4)	(12·2)	(0·4)	(0·1)
FEMALES	13·4	4·8	103·0	160·4	4·1	110·4	2·4	1·0
	(1·9)	(0·5)	(39·2)	(9·6)	(0·4)	(12·8)	(0·5)	(0·2)
Free-living sample (Bush, unpubl. data)								
MALES	13·5	6·2	180·3	159·6	4·7	112·9	2·4	0·9
	(3·9)	(0·6)	(49·8)	(3·7)	(0·4)	(3·1)	(0·2)	(0·1)
FEMALES	17·3	5·9	160·0	157·0	4·7	92·7	2·3	0·9
	(2·7)	(0·6)	(57·6)	(4·2)	(0·4)	(38·7)	(0·2)	(0·2)
Captive 'British' sample (Kock, unpubl. data)								
MALES	14·5	–	201·9	159·3	3·8	125·3	2·6	–
	(5·1)		(73·7)	(2·3)	(0·3)	(3·6)	(0·1)	
FEMALES	13·7	–	253·0	157·9	3·7	122·4	2·6	–
	(2·5)		(84·9)	(1·8)	(0·2)	(2·9)	(0·1)	
Captive 'ISIS' sample (1984)								
MALES	–	9·3	184·8	161·0	5·0	121·0	2·7	–
		–	–	–	–	–	–	
FEMALES	–	8·7	228·8	158·0	4·9	122·0	2·7	–
		–	–	–	–	–	–	

All values in S.I. units. Conversion factors used were: urea, mg/100 ml × 0·357; glucose, mg/100 ml × 0·0556; creatinine, mg/100 ml × 88·0; sodium, potassium, chloride, meq/l × 1·0; calcium, mg/100 ml × 0·250; magnesium, mg/100 ml × 0·417

Comparison of free-living and captive animals

Free-living females were found to have macrocytic red cells compared to captive females, and both sexes in the free-living sample showed slight monocytosis. Although no blood-borne parasites were found, and trypanosomiasis has not been found in cheetahs (Kingdon, 1977), in contrast to lions (C. Packer, pers. comm.), both parasites and ticks can cause mild anaemia, manifest as macrocytosis as a result of erythroid stimulation. Rickettsial disease can sometimes induce monocytosis as well. All the free-living animals showed anisocytosis which can be associated with mild anaemia. Moreover, *Ancylostoma* infestation, which is found in most of the free-living cheetahs, can cause anaemia in felids and canids, and could, in part, explain the difference between captive and free-ranging animals as this parasite has not been found in cheetahs captive in Britain. Interestingly, *Toxocara* eggs are frequently found in the faeces of most captive cheetahs and infestations are often associated with mortality in neonates, yet no *Toxocara* eggs were found in the faecal samples of free-living individuals, despite the inclusion of a lactating female where infection might be expected.

The captive samples had higher levels of both glucose and creatinine than the free-ranging animals, possibly reflecting a higher food intake. For example, over the course of seven days, two adult females at Whipsnade Zoo were each fed an average of 1·7 kg per day (S.D.s = 0·2, 0·4), while an adult male was fed 2·1 kg per day (S.D. = 0·2) (G. Lucas, pers. comm.). However, by observing cheetah mothers (only some of whom were lactating) over the course of 1–7 consecutive days in the Serengeti, and by selecting only those families where all the kills that the mother made over the observation period were known, it was possible to calculate the kilograms of food that mothers ate by dividing the amount of flesh consumed on each carcass (Blumenschine & Caro, 1986) by the percentage of time mothers spent eating compared to their cubs. Mothers, whose energy needs are presumably greater than the captive non-mothers, and who usually move considerably further than captive animals, ate only an average of 1·3 kg of meat per day (range 0·3–3·4 kg/day), or about 75% of the captive diet.

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