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Abstract: Information regarding morphology of wild cheetahs is scant, and even where data exist they rarely were collected using a standardized methodology. We used a consistent technique to examine 241 wild Namibian cheetahs *(Acinonyx jubatus jubatus)* to study morphology, sexual dimorphism, growth rates, and physical condition and to investigate how these data compared with those in previous studies. Significant sexual dimorphism was evident for all measurements. The majority of cheetahs were in excellent condition at the time of examination, although old cheetahs and those that had been held captive for more than a month were in significantly poorer condition. Both male and female cheetahs reached adult body mass at 49-96 months of age. These data differed significantly from those collected during other studies, although such differences may be due to variations in collection methodology. It is therefore vital to standardize morphometric data collection techniques so that the true extent of differences between populations can be assessed more accurately. A suggested standardized collection methodology is presented.

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MORPHOLOGY, PHYSICAL CONDITION, AND GROWTH OF THE CHEETAH (*ACINONYX JUBATUS JUBATUS*)

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Information regarding morphology of wild cheetahs is scant, and even where data exist they rarely were collected using a standardized methodology. We used a consistent technique to examine 241 wild Namibian cheetahs (*Acinonyx jubatus jubatus*) to study morphology, sexual dimorphism, growth rates, and physical condition and to investigate how these data compared with those in previous studies. Significant sexual dimorphism was evident for all measurements. The majority of cheetahs were in excellent condition at the time of examination, although old cheetahs and those that had been held captive for more than a month were in significantly poorer condition. Both male and female cheetahs reached adult body mass at 49–96 months of age. These data differed significantly from those collected during other studies, although such differences may be due to variations in collection methodology. It is therefore vital to standardize morphometric data collection techniques so that the true extent of differences between populations can be assessed more accurately. A suggested standardized collection methodology is presented.

Key words: *Acinonyx jubatus*, cheetah, growth, measurement protocol, morphometrics, physical condition

The cheetah (*Acinonyx jubatus*) is the world's fastest land animal and is highly specialized for speed in terms of anatomy, physiology, and behavior (Ewer 1973; Gray 1968). Films of cheetahs running show an acceleration from 0 to 80 km/h in just 3 strides, with the maximum speed of 110 km/h being attained in a few seconds (Hildebrand 1959, 1961). Such impressive physiological ability is the result of a highly specialized morphology, including a lightweight skeleton, long foot and leg bones, and a small, aerodynamically efficient frame. The skull is small and thin-boned, and the face is relatively flat with a reduced muzzle length that allows the large eyes to be positioned for maximum binocular vision (Ewer 1973). To rapidly alleviate the high-oxygen debt accumulated through high-speed chases, the nostrils are enlarged and the sinuses are extensive and air-filled (Ewer 1973; Guggisberg 1975). In an evolutionary trade-off, the small skull cannot support a large masseter bulk, and the enlarged nasal cavity does not leave room for long root canals, so the jaws are weak, and the canine teeth are small compared with those of other large cats. As a consequence, the cheetah is poorly equipped to defend itself or its kills from other large, more powerful predators (Caro 1994).

This uniquely specialized felid once ranged across Asia, India, the Middle East, and Africa (Myers 1975) but now occurs only in a fraction of its historic range (Marker 1998). Today, most taxonomists recognize 5 subspecies, although the extent of morphological differences among subspecies is uncertain, and information from genetic studies indicates that cheetahs as a

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species are exceptionally uniform (Menotti-Raymond and O'Brien 1993; O'Brien et al. 1983, 1985, 1987). Certain physical abnormalities, such as the presence of a kink in the last few caudal vertebrae, crowded lower incisors, and focal palatine erosion, have been reported in the Namibian cheetah (*Acinonyx jubatus jubatus*) population, and these may be linked to an unusually low level of genetic diversity (Berry et al. 1997; Marker-Kraus 1997).

Detailed information about the morphology of wild *A. j. jubatus* is sparse but shows regionalized variation. Morphology has been described in several studies from different regions of Africa, including East Africa (Caro 1994; Caro and Collins 1987; McLaughlin 1970), South Africa (Labuschagne 1979; McLaughlin 1970), and Namibia (du Preez 1976), but only one of these studies (Caro 1994; Caro and Collins 1987) involved a large data set. We collected morphometric data for 241 cheetahs from across Namibia during an 8-year period, making this the most comprehensive morphologic study to date.

We present data on the morphology of Namibian cheetahs and compare our results with those from other studies in southern and East Africa to examine the extent of morphological differences. Growth curves for wild cheetahs are presented, and the physical condition, growth, and morphology are all investigated in relation to age and sex. In addition, comprehensive measurement guidelines that can be used in future studies are defined. Our use of this standard measurement protocol on a large sample size should provide valuable information regarding the morphology, sexual dimorphism, physical condition, and growth of wild cheetahs and provide a solid base for comparisons with other studies.

Materials and Methods

Cheetahs were livetrapped or killed on farmlands in Namibia, from 19°30′ to 23°30′S and 16° to 19°E, between 1991 and 1999. The capture cages used to livetrap cheetahs usually measure 2 by 0.75 m by 0.75 m, with trap release doors at each end and a trigger plate in the middle. Live cheetahs were immobilized either in the capture cage or in our squeeze and transport crate using either a hand syringe or a blowpipe. Animals in a holding compound were darted using an air-pump dart gun or a blowpipe (Telinject GMBH, Roemerberg, Germany). In all immobilizing procedures, anesthesia was administered intramuscularly in the hindquarters with Telazol (tiletamine HCl and zolazepam HCl; Warner Lambert, Ann Arbor, Michigan) 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. Dead cheetahs were collected and brought to the Cheetah Conservation Fund (CCF) headquarters, where they were examined and the skeletons subsequently kept in storage. Only live or very recently deceased, intact cheetahs were used for morphological analyses.

Under anesthesia, a thorough physical examination was performed, and each cheetah was placed in one of the following 3 categories depending on condition, musculature, body fat, injuries, and external parasites: excellent—robust, healthy coat; fair—not robust, poor hair coat; and poor—sores, moderate to severe medical problems. Superficial wounds sustained in the capture cage were not considered while allocating categories because they were not considered to be natural.

Cheetahs were assigned to one of 8 age-class categories, using both sets of criteria shown in Appendices I and II. Age classification (Appendix I) was based on the descriptions from previous studies and on personal experience (Blueweiss et al. 1978; Burney 1980; Caro 1994) and took into account weight (Appendix II), tooth wear, gum recession, wear on pads, pelage, scarring, body size, social groupings of animals caught together, and reproductive condition. Accuracy of these criteria was tested by comparing these estimated ages with age categories determined from examination of cementum layers of the lower premolars of dead cheetahs (Matson's Laboratory, LLC, Milltown, Montana). Cheetahs in the first 3 classes in Appendix II were considered to be dependent on their dam and were categorized as juveniles. For this study, only measurements and masses recorded from animals held <30 days in captivity were used because they were hypothesized to be representative of the wild situation.

In many cases, cheetahs were held captive for some time before CCF was contacted, so the number of days the animals were held in captivity before examination was recorded. Measurements for adult animals were included only when the individual had been caught as an adult (defined as >30 months old), to give a more accurate indication of the normal measurements for wild cheetahs without influence from development in a captive situation. Data were not included if the age group was not known.

Morphometric data were collected on the following 16 variables: body mass—measured using a hanging balance, with the cheetah placed in a sling; total body length—tip of nose to end of last caudal vertebra; head–body length—tip of nose to base of tail, measured to notch on sacrum; tail length—base of tail (sacrum) to end of last caudal vertebra; skull length—from top of occipital bone, which can be felt as a notch on back of skull, to tip of nose; skull width—greatest width at zygomatic arches; muzzle girth—circumference with mouth fully closed; canine length—from gum line to tip of C1 and c1; chest girth—widest point of thorax; girth of abdomen—immediately anterior to hind legs at narrowest point; total length of foreleg—most dorsal point of scapula to base of foot, measured to posterior aspect of plantar pad; total length of hind leg—top of ileum (most dorsal point of hip) to base of foot; foot width—widest point of foot; foot length—back of palmar pad to tip of digital pad; width of testis—at widest part of testis; and length of testis—from base of testis measured laterally. For variables measured on both sides of the body, such as tooth, leg, foot, and testis measurements, the mean of both sides was used for analyses. There was some variation in sample size for each parameter measured because it was not always possible to measure every variable on every cheetah examined due to factors such as rapid recovery from anesthesia or injury to a particular body part.

Vernier calipers were used to record skull length, skull width, muzzle length, tooth lengths, and foot measurements, and they allowed measurements to be recorded to 0.1 cm. All other measurements aside from body mass were taken using a 200-cm measuring tape and were recorded to the nearest 1.0 cm. Body mass was recorded to the nearest kilogram. Leg measurements were taken while the legs were positioned as if the cheetah was taking a normal step.

Rates of growth were estimated from measuring cubs of different ages and from multiple examinations of individual cubs as they aged. As the rate of development in a captive situation may not be parallel to that in the wild, only data from cubs that had been held captive for <30 days before examination were used.

To investigate whether there were spatial differences in morphology, we compared the cheetahs captured in different regions of the country, using accepted national regions as designated by the Ministry of Agriculture (Schneider 1994). Temporal differences also were investigated by analyzing results collected across seasons and years. Namibia has 3 seasons as described by Berry (1980), 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 CCF's Waterberg Plateau study area over a 40-year period was 123.4 mm for the hot dry season, 348.6 mm for the hot wet season, and 2.8 mm for the cold dry season.

Data were analyzed using SPSS PC version 10.0.5 software for Windows 95/98 and NT (SPSS Inc., Chicago, Illinois). Assumptions of normality were tested using the Kolmogorov–Smirnov and Shapiro–Wilk statistical tests, and in cases where the data deviated significantly from a normal distribution, parametric tests were replaced with nonparametric equivalents. Statistical techniques used included single-factor analysis of variance, Student's t-tests, independent samples t-tests using Levene's test for equality of variances, and the nonparametric Mann–Whitney and Kruskal–Wallis tests. Additionally, a regression analysis was used to describe the relationship between body weight and chest girth, according to Currier (1979). Results were considered significant at $P < 0.05$, and all tests were 2-tailed unless otherwise stated.

Results

Samples were categorized by sex and age group (Table 1). Significant sexual dimorphism, with males being larger, was evident for all measurements recorded (Table 2). There was a significant difference between the mean weights of males between years ($F = 2.880$, $d.f. = 8$, $P = 0.007$) but not

TABLE 1.—Numbers of male and female cheetahs examined and categorized by age group. This included both "wild" (captive <30 days) and "captive" animals (held for ≥30 days before examination). Percentages refer to the proportion of the total sample population that was contributed by each age group.

Age group (months)	Male	Female	Percentage
0–6	10	10	8.3
>6–12	20	21	17.0
>12–18	13	7	8.3
>18–30	17	6	9.5
>30–48	46	9	22.8
>48–96	47	24	29.5
>96–144	5	5	4.1
>144	1	0	0.4
Total	159	82	99.9

for females (F = 1.136, *d.f.* = 8, P = 0.368).

Cheetahs were captured in 7 different geographical regions (n ranged from 6 to 80 cheetahs), and there were no significant differences in adult body mass among either males or females, or among regions (males: F = 1.51, *d.f.* = 9, P = 0.165; females: F = 1.63, *d.f.* = 6, P = 0.173). There was no significant effect of seasonality on body mass for adult males or females (males: F = 1.715, *d.f.* = 2, P = 0.185; females: F = 0.273, *d.f.* = 2, P = 0.763). Those considered "captive" at the time of examination, i.e., those that had been captive for ≥30 days, weighed less than the "wild" individuals, although the difference was not statistically significant for either sex (males: F = 3.034, *d.f.* = 1, P = 0.084; females: F = 0.294, *d.f.* = 1, P = 0.591).

Physical condition.—Scores for physical condition were assigned to 240 animals (99.6%), of which 63% (n = 151) were in excellent condition, 22.9% (n = 55) in fair condition, and 14.2% (n = 34) in poor condition. Overall there was no significant relationship between physical condition and sex (z = −0.76, P = 0.449), season (χ^2 = 1.213, *d.f.* = 2, P = 0.545), or region (χ^2 = 8.803, *d.f.* = 9, P = 0.456). There also was no overall relationship between age and physical condition (χ^2 = 9.326, *d.f.* = 7, P = 0.230), although old and very old adults (those >96 months of age) were found to be in significantly poorer condition than younger individuals (z = −2.96, P = 0.003). Cheetahs that had been held captive for ≥30 days were in significantly poorer physical condition (z = −2.40, P = 0.016).

The ratio of weight to length varied significantly among physical condition groups for adult wild-caught individuals (χ^2 = 16.248, *d.f.* = 2, P < 0.001), with those in excellent physical condition having significantly higher ratios than those in other conditions (z = −4.00, P < 0.001). This ratio (Fig. 1) was not significant between those in fair versus poor condition (z = −0.98, P = 0.328).

Growth curves.—Adult body mass was not achieved until age group 6 (49–96 months old) in either sex (Fig. 2). Growth curves for both body mass and body length are presented in Fig. 3, using data from cubs (≤12 months old) that had been held captive for <30 days (range 1–13 days in captivity, mean 4.3 days for males; range 0–14 days in captivity, mean 4.6 days for females). There was no significant difference in the length of time male and female cubs had been held in captivity (t = 0.345, *d.f.* = 51, P = 0.732). Using a power equation, where y = body mass (in kg) and x = chest girth (in cm), a close correlation was found between chest girth and body mass: $y = 0.727x + 38.533$, R^2 = 0.888.

DISCUSSION

Physical condition.—The large home ranges of Namibian cheetahs (Marker 2000) and the homogeneity of the semiarid farmland environment suggest that the Namibian population is exposed to similar habitats and prey across different geographic regions. There would therefore appear to be no selective pressure for varying physical condition or body mass between seasons or regions of the country. Physical condition

TABLE 2.—Morphometric data for the wild adult cheetahs (aged >30 months at capture and held in captivity for <30 days). Statistical tests were conducted to ascertain the degree of sexual dimorphism exhibited for each parameter.

Measurement	Adult male					Adult female					Sexual dimorphism	Test[a]	Statistic	*d.f.*	*P*
	$\bar{X}$	Low	High	*SD*	*n*	$\bar{X}$	Low	High	*SD*	*n*					
Body mass (kg)	45.6	31.0	64.0	5.99	99	37.2	26.0	51.0	5.14	38	22.7	1	−7.67	135	<0.001
Upper canine length (cm)	2.2	1.6	2.6	0.20	87	2.1	1.7	2.3	0.16	37	5.3	2	−2.93		0.003
Lower canine length (cm)	1.6	1.0	2.1	0.23	86	1.4	1.0	2.0	0.22	35	9.5	2	−3.27		0.001
Skull length (cm)	23.4	21.0	26.7	1.27	54	21.8	18.5	24.1	1.43	26	7.3	1	−5.10	78	<0.001
Skull width (cm)	14.6	12.4	17.2	0.86	84	13.3	10.8	14.7	0.75	37	10.2	1	−8.30	119	<0.001
Muzzle girth (cm)	28.0	16.0	33.0	2.14	83	26.1	23.0	30.0	1.51	36	6.9	2	−5.19		<0.001
Chest girth (cm)	71.7	64.0	83.0	3.86	90	67.3	56.0	75.0	3.76	38	6.5	2	−5.28		<0.001
Abdomen girth (cm)	59.4	46.0	81.0	5.67	89	54.0	44.0	68.0	5.01	38	10.0	1	−5.10	125	<0.001
Body length (cm)	125.5	108.0	152.0	7.03	94	120.1	105.0	135.0	5.91	38	4.5	1	−4.14	130	<0.001
Tail length (cm)	76.7	51.0	87.0	5.17	94	72.5	57.0	79.0	4.83	39	5.9	2	−4.79		<0.001
Total length (cm)	202.2	167.0	226.0	9.38	94	192.4	162.0	214.0	9.53	38	5.1	2	−5.28		<0.001
Total foreleg length (cm)	77.0	71.0	86.0	3.07	85	73.6	62.0	80.0	3.58	38	4.6	1	−5.34	121	<0.001
Total hind leg length (cm)	81.1	73.0	89.0	3.21	86	77.8	69.0	83.0	2.80	38	4.2	2	−5.12		<0.001
Front foot length (cm)	8.2	6.8	9.8	0.47	87	7.8	6.8	9.0	0.46	38	4.7	2	−4.29		<0.001
Front foot width (cm)	6.1	5.2	7.2	0.40	87	5.7	4.9	6.6	0.40	38	7.1	1	−5.25	123	<0.001
Hind foot length (cm)	9.2	8.0	10.3	0.49	86	8.8	7.0	9.7	0.51	38	3.8	2	−3.40		0.001
Hind foot width (cm)	6.2	4.9	8.0	0.46	86	5.9	4.9	7.0	0.48	38	5.3	1	−3.41	122	0.001
Testis length (cm)	2.8	1.9	3.8	0.49	81										
Testis width (cm)	2.0	1.5	2.6	0.23	83										

[a] Test 1 = independent samples *t*-test (test statistic = *t*), and test 2 = Mann–Whitney *U*-test (test statistic = *z*).

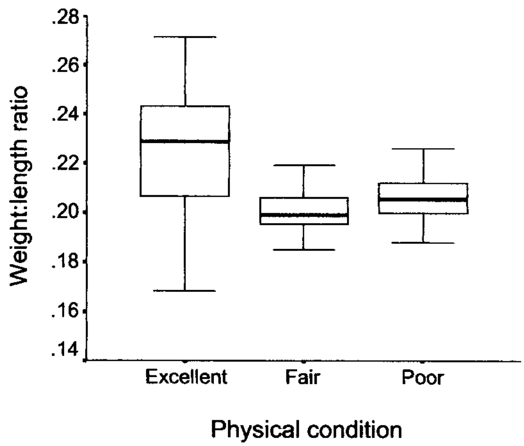

FIG. 1.—Ratios of weight to length for adult cheetahs in excellent, fair, and poor physical conditions. Data were restricted to cheetahs that were captured as adults (>30 months old) and those that were considered to be wild at the time of examination (held in captivity for <30 days). Box represents middle 2 quartiles, vertical line shows 1st and 4th quartiles, and horizontal line denotes median.

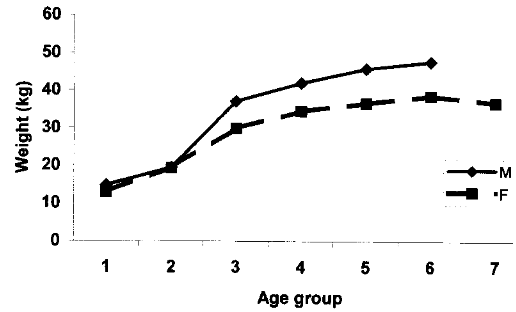

FIG. 2.—Body mass of male and female cheetahs by age group. Data were restricted to wild animals (i.e., those held in captivity for <30 days).

did not vary between age groups except for older individuals (>96 months) and those held in captivity for an extended time (≥30 days). Older animals, both males and females, were in significantly poorer physical condition. For females this may be a result of the increased physiological stresses from rearing young, similar to that reported in studies of mountain lion (Charlton et al. 1998; Roelke et al. 1985), whereas for males this may be a result of territorial fighting. Additionally, many of the older individuals examined, both males and females, were found to have had teeth broken, which could have contributed to their poorer physical condition.

As a specialized sprinter and hunter, the cheetah's physiological makeup may need a certain amount of regular exercise to maintain optimal physical health. Studies conducted on captive cheetahs have shown a variety of health problems and stress-related diseases that may be linked to low levels of exercise (Munson 1993; Munson et al. 1999; Terio 2000). Although our study only presents scores for physical condition rather than an in-depth analysis, those held in captivity for extended lengths of time (≥30 days) were in significantly poorer physical condition than others. This could potentially predispose them to disease problems in

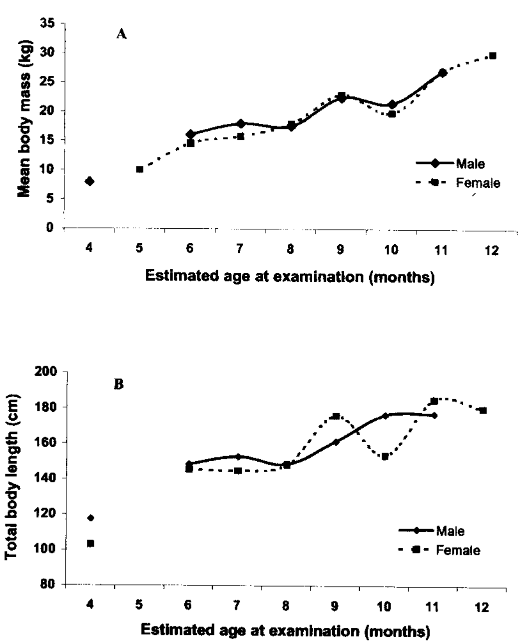

FIG. 3.—Growth curves for 25 male (continuous line) and 28 female (broken line) cheetah cubs held in captivity for <30 days. Values represent the mean for all cheetah cubs in that age group. A) Body mass. B) Body length. Sample sizes ranged from 2 to 7 cheetahs for each age.

TABLE 3.—Morphometric data for cheetahs published from various studies on 2 subspecies of *Acinonyx jubatus*. All measurements are in centimeters, apart from mass (in kg). Superscript numbers denote significant variation from other studies: 1, from this study; 2, from du Preez (1976); 3, from Labuschagne (1979); 4, from McLaughlin (1970); 5, from Caro (1994); and 6, from McLaughlin (1970).

Body measurement	Mean (this study) *A. j. jubatus*	Etosha N.P.[a] Namibia (du Preez 1976) *A. j. jubatus*				Kalahari Gemsbok N.P. South Africa (Labuschagne 1979) *A. j. jubatus*			
		$\bar{X}$	*n*	Min.	Max.	$\bar{X}$	*n*	Min.	Max.
Male mass	45.6[4,5,6]	44.1	8	38.6	57.6	53.9	7	39	59
Female mass	37.2[4,6]	35.9	8	29.5	44.5	43.0	6	36	48
Male total length	202.2[5,6]	202.4	10	194.4	222.3	206.0	7	191	221
Female total length	192.4[6]	193.1	10	179.7	210.8	190.0	7	184	196
Male body length	125.5[5]	130.8	10	126.4	141.0				
Female body length	120.1[5]	124.8	10	117.5	134.6				
Male tail length	76.7[5]	71.6	10	68.0	81.3	71.5	7	65	76
Female tail length	72.5[5]	68.3	10	62.2	76.2	66.7	6	63	69
Male chest girth	71.7[5]	70.1	10	66.0	78.7				
Female chest girth	67.3[4,6]	63.0	10	54.6	69.9	43.0	6	36	48
Male shoulder height	77.0[4]	85.7	10	78.7	96.5	88.1	7	83	94
Female shoulder height	73.6	80.8	10	73.7	69.9	84.7	6	79	84

[a] N.P., National Park.

the future (Munson and Marker-Kraus 1997).

Growth curves.—Growth curves indicate that individuals continue to grow until they reach >49 months of age. This is comparable with the age when females and males reach their prime, are fully developed and muscled, and when males are able to hold and defend territories (Caro 1987). Quantifying relationships between body size and various other parameters have been presented for a number of species to help predict certain ecological and physiological characteristics (Bailey 1968; Blueweiss et al. 1978; Charlton et al. 1998; Robinson 1960). In our study, assessment of scores for physical condition of individual animals corresponded well with ratios of body weight to length.

(Currier 1979) presented a useful correlation between chest girth and body weight of pumas that could be used when scales are not available. This correlation also has been used in other species (Beger and Peacock 1988; Charlton et al. 1998; Durner and Amstrup 1996; Millspaugh and Brundige 1996) and showed a good correlation for cheetahs in this study. Therefore, chest girth may be used to accurately estimate weight in the field.

Comparisons with other studies.—Both sexes of cheetahs measured in this study were significantly heavier than the measurements recorded for captive cheetahs in North American zoos (Wildt et al. 1993—captive males, mean mass = 40.2 kg: t = 9.05, *d.f.* = 98, P = 0.000; captive females, mean mass = 35.0 kg: t = 2.65, *d.f.* = 37, P = 0.012). This followed the trend seen throughout this study, where cheetahs held captive for a month or more were lighter than their wilder counterparts, although the difference was not statistically significant. The cheetahs examined in this study showed significant sexual dimorphism for all parameters measured, which differed from the Serengeti cats that exhibited dimorphism only in body mass, chest girth, and tail length (Caro 1994). There also were significant differences in most of the variables measured among all the published studies (Caro 1994; du Preez 1976; Labuschagne 1979; McLaughlin 1970). These differences may reflect local adaptations to

TABLE 3.—Extended.

South Africa (McLaughlin 1970a) *A. j. jubatus*				Serengeti N.P. (Caro 1994) *A. j. raineyii*				East Africa (McLaughlin 1970b) *A. j. raineyii*			
$\bar{X}$	n	Min.	Max.	$\bar{X}$	n	Min.	Max.	$\bar{X}$	n	Min.	Max.
55.0[1,5,6]	4	50	62	41.4[1,4,6]	23	28.5	51.0	61.0[1,4,5]	4	58	65
48.5[1,5]	2	39	58	35.9[4,6]	19	21.0	43.0	52.0[1,5]	2	41	63
201.3[5,6]	14	179	222	190.6[1,4,6]	24	172.0	209.5	209.4[1,4,5]	5	198	224
186.0	1			189.8[6]	16	174.0	208.0	207.4[1,5]	5	191	236
				122.5[1,6]	24	113.0	136.0	127.0[5]	2	124	130
				124.5[1]	16	113.0	140.0				
72.8[5]	6	60	79	68.1[1,4]	24	63.0	74.0	66.0	1		
				65.5[1]	19	59.5	73.0	73.0	1		
				69.2[1]	21	62.0	77.0				
48.5[1,5,6]	2	39	58	66.2[4,6]	12	61.0	72.0	52.0[1,4,5]	2	41	63
79.9[1]	8	74	86					76.8	6	74	81
70.0	1							75.3	3	67	84

environmental conditions, e.g., climate, latitude, prey type, and prey availability, but also may reflect differences in measurement protocols and sample sizes.

Results from this study were compared with those found elsewhere (Caro 1994; du Preez 1976; Labuschagne 1979; McLaughlin 1970). There were significant differences among studies for every parameter measured except for female shoulder height (Table 3) even when examining individuals of the same subspecies, suggesting that it may be the measuring protocols as much as the actual body measurements that differ significantly among studies.

Compared with the South African population of *A. j. jubatus* (McLaughlin 1970), Namibian cheetahs were smaller for some variables but larger for others. Sample sizes in the South African study were often small, and this may be a source of bias. When compared with results from the Serengeti (Caro 1994), Namibian cheetahs were larger than their East African (*A. j. raineyii*) counterparts. However, the East African cheetahs examined by McLaughlin (1970) were significantly larger than those measured by Caro (1994) for all parameters except female chest girth. When the CCF data were compared with McLaughlin's (1970) results, East African cheetahs appeared to be longer and heavier than those in Namibia, although females had a smaller chest girth.

McLaughlin (1970) studied both East and South African cheetahs and reported no significant differences between the 2 subspecies for all measurements taken except total length for males, where the East African males were longer. However, the data reported by McLaughlin (1970) may be misleading because they relied on very small sample sizes (1–6 animals), whereas Caro's data were more comprehensive, with sample sizes ranging from 12 to 24 animals; the data in this study rely on still larger samples. Because of the larger sample sizes, we believe that Caro's (1994) results are more likely to be representative of the normal measurements of *A. j. raineyii.*

The Namibian cheetahs measured in this study were larger than the Serengeti cheetahs but generally were smaller than the East African cheetahs measured by Mc-

Laughlin (1970). Because of such discrepancies, it is difficult to make any conclusions about the extent of morphometric variations among the different subspecies. The fact that McLaughlin's (1970) results show little variation between East and South African subspecies, presumably using the same measurement techniques, again suggests that differences in results between studies could be due as much to variation in measurement protocols as to actual subspecific variation. McLaughlin's (1970) data are hampered by small sample sizes, and because of this, we consider Caro's (1994) study to be more representative of the normal measurements of *A. j. raineyii*.

Various authors have hypothesized about the possible causes of size variation within species, with factors such as climate, prey base, and competition from other predators being of probable importance (Gittleman 1985; James 1970; McNab 1971). An in-depth discussion of potential mechanisms goes beyond the scope of this study, and for further discussion, interested readers should consult Gay and Best (1996).

A study by O'Brien et al. (1987) revealed that the 2 subspecies *A. j. jubatus* and *A. j. raineyii* are genetically very similar, being separated by a Nei genetic distance of 0.004. This extreme uniformity questions the validity of classifying them as separate subspecies based on genetic data. In addition, it is difficult to establish the degree of morphological variation without using a standardized methodology. Therefore, it is important to standardize techniques for gathering morphometric data, and for authors to state clearly how their data were collected. This study presents a clear methodology to be used for measuring cheetahs, which, if adopted as a standard in future research, would make it easier to directly compare morphological variation among different populations.

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APPENDIX I

The following physical characteristics were used to assign cheetahs in this study to age categories.

Young cubs (0–6 months old).—Deciduous canines and incisors erupt at 28–30 days; molars erupt at 45–50 days. Spots on legs and yellow hair coloring develop at 6–7 weeks, mantle is present from 4 weeks and is lost at 3–4 months. Eyes open at 7–10 days, cubs emerge from den at about 6 weeks.

Large cubs (6–12 months old).—Lower incisors fall at about 7 months, adult teeth erupt at about 8 months. Long hair on back of neck still remains, although it is no longer a defined mantle. Lanky appearance until about 9 months, then body begins to fill out; body mass about two-thirds by 12 months.

Adolescents (12–18 months old).—No tartar or yellowing of teeth. Some long fur on back of neck; fur on face and body fuzzy and scruffy rather than smooth. Attain full height but not adult weight; leggy; still with dam.

Newly independent (18–30 months old).—No tartar or yellowing of teeth. Some long fur on back of neck; smooth, sleek coat. Develop muscle tone; usually not with dam but may be with littermates.

Young adults (30–48 months old).—Slight tartar and yellowing of teeth. Slight mane still; males have scars, females usually pregnant or with cubs. Fully grown but not fully muscled, in prime physical condition.

Prime adults (48–96 months old).—Tartar and yellowing of teeth, slight gum recession, some gingivitis. Mane on back of neck is gone. Fully muscled, prime physical condition but starting to show signs of aging.

Old adults (96–144 months old).—Tartar and yellowing of teeth; gum recession; gingivitis; canines tipped; loss of teeth, especially incisors. Coat beginning to look ragged, poorly groomed, scarred. Pads becoming smooth and elongated, sunken face, thinner, loss of muscle tone.

Very old adults (>144 months old).—Tartar and yellowing of teeth; gum recession; gingivitis; canines tipped; loss of teeth, especially incisors and canines; broken teeth. Ragged, poorly groomed, scarred coat. Pads quite smooth and elongated, sunken face, body delicate and frail.

Appendix II

Approximate body measurements used as part of the methodology for categorizing cheetahs into age classes.

Class	Age (months)	Weight (kg)		Length (cm)		Chest girth (cm)	
		Males	Females	Males	Females	Males	Females
Young cubs	0–6	<19	<18	<96	<92	<54	<54
Large cubs	>6–12	12–31	12–30	84–120	82–114	42–61	40–57
Adolescents	>12–18	30–38	25–35	110–133	105–125	60–76	56–64
Newly independent	>18–30	35–48	28–38	119–129	116–130	64–71	63–66
Young adults	>30–48	39–56	30–41	115–140	113–126	64–83	64–89
Prime adults	>48–96	37–58	31–52	118–137	115–126	66–80	63–75
Old adults	>96–144		26–48		105–131		
Very old adults	>144						